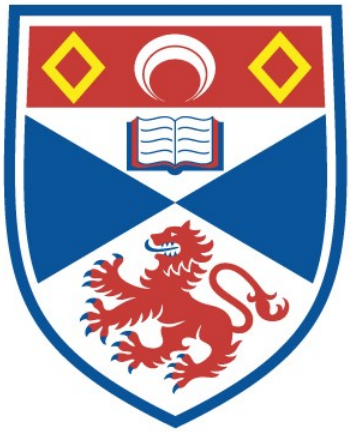
THE IMPACT OF RIVER FLOW ON THE DISTRIBUTION AND ABUNDANCE OF SALMONID FISHES

Andrew Mark Warren

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



2017

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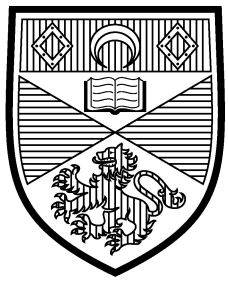

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Faith: not wanting to know what the truth is

Friedrich Nietzsche (1882)

Abstract

River flow regime is fundamental in determining lotic fish communities and populations, and especially of salmonid fishes. Quantifying the effects of human induced flow alteration on salmonids is a key question for conservation and water resources management. While qualitative responses to flow alteration are well characterised, a more intractable problem is quantifying responses in a way that is practical for environmental management.

Using data drawn from the Environment Agency national database, I fitted generalised linear mixed models (GLMMs) using Bayesian inference to quantify the response of salmonid populations to the effects of impounding rivers, flow loss from rivers due to water abstraction, and the mitigating effects of flow restoration.

I showed that in upland rivers downstream of impounded lakes, the magnitude of antecedent summer low flows had an important effect on the late summer abundance of 0+ salmonids Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). In contrast, the abundance of 1+ salmon and brown trout appeared to be largely unresponsive to the same flows. I demonstrated that short-term flow cessation had a negative impact on the abundance of 1+ brown trout in the following spring, but that recovery was rapid with negligible longer-term consequences. I further established that flow restoration in upland streams impacted by water abstraction provided limited short-term benefits to salmonid abundance when compared with changes at control locations. However, while benefits to salmonid abundance were limited, I detected important benefits to the mean growth rates of 0+ and 1+ brown trout from flow restoration.

I discuss the implications of my findings for salmonid management and conservation and propose a more evidence-based approach to fishery management based on robust quantitative evidence derived using appropriate statistical models. The current approach to flow management for salmonids requires revision and I recommend an alternative approach based on quantitative evidence.

Acknowledgements

Although producing a thesis is often viewed as a solo effort, most, including this one, rely upon a support network largely unseen by examiners and others who may read it. My immediate thanks go to my supervisor, Carl Smith, whose constant and steady guidance and experience helped me negotiate the whole PhD process and produce this thesis. Carl, along with Rowena Spence, also provided support on a number of levels beyond purely academic, and for that I am grateful and eternally indebted. Numerous colleagues at the Environment Agency have also supported me and could see the benefits of tackling this subject for the organisation and for my own development. In that regard my thanks go to Mike Dunbar, Phil Humble, Paul Sadler and Tim Webb for all you've done, and tried to do for me throughout the life of this PhD.

Any support structure needs a firm foundation and my family have been just that. My wife Beth and children Eirlys and Ffion have suffered my frustrations and absence throughout and with good humour. They help keep life in perspective and part of that is the importance of self-improvement and advancement of skills and knowledge. I love you and know how lucky I am to have such a wonderful family.

Data acknowledgements

I am grateful to the Environment Agency for allowing access to the river flow and salmonid survey data for use in my research. I also acknowledge the survey teams undertaking the sampling of salmonids, the staff who collate and manage the National Fisheries Population Database (NFPD) and the hydrology staff who collect and collate river flow data, without their contribution there would be no data by which to test hypotheses.

Contents

PREAMBLE

River flow regime is widely acknowledged as key to shaping lotic fish communities and populations (Poff et al., 1997). Given the degree to which man has sought to manage river flows, recognising the effects of flow on fish is a pressing question for conservation and resource management. While a qualitative understanding of how flow regime can impact fish is well characterised, a more intractable problem is quantifying flow effects in a way that is practical for fisheries and ecosystem managers (Warren et al., 2015).

AIMS OF THE THESIS

In this thesis I seek to fit the most appropriate statististical models to quantify the consequences of flow management on fish distribution and abundance, with a focus on salmonid fishes. In **Chapter 1** I begin by presenting a comprehensive review of the current literature on the effects of flow on salmonid fishes. Throughout this thesis I have used Bayesian inference in approaching my data analyses. In **Chapter 2** I set out the strengths and potential weaknesses of Bayesian inference and argue why it has particular utility in ecological management. In the subsequent four chapters I examine the impacts of three scenarios confronting fishery managers: the effects of impounding rivers, flow loss from rivers due to water abstraction, and the mitigating effects of flow restoration. In **Chapter 3** I model the response of juvenile (0+ and 1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) abundance to antecedent flows downstream of impounded lakes used for water abstraction. **In Chapter 4** I examine the effect of a short-term cessation of reservoir compensation flow using a Before–After Control–Impact (BACI) design to test for impacts on 1+ brown trout abundance and subsequent recovery. In **Chapter 5** I investigate the effects of flow restoration on the

over-summer survival of 0+ and 1+ brown trout and Atlantic salmon in upland rivers that have historically experienced low summer flow as a result of impoundment and water abstraction. In **Chapter 6**, using the same study described in **Chapter 5**, I model the effect of flow restoration on the mean growth rate of 0+ and 1+ brown trout. Finally, in **Chapter 7** I consider the implications of my findings for salmonid management and conservation and propose a more evidence-based approach to fishery management based on robust quantitative evidence.

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Chapter One

RIVER FLOW AS A DETERMINANT OF SALMONID DISTRIBUTION AND ABUNDANCE

ABSTRACT

River flow regime can have a fundamental effect on riverine biota. It influences key aquatic processes, including levels of dissolved oxygen, sediment transport and deposition, water quality and habitat type and distribution. In this chapter I review the impact of flow on the abundance and distribution of salmonid fishes in the context of developing approaches to regulating, setting and restoring river flow regimes as a means of conserving and managing populations. Flow can have direct impacts on salmonids, both through peak flow resulting in the washout of juveniles, and stranding of all life stages under low flow conditions. Salmonids can also be adversely affected through indirect effects of flow, from impacts on water temperature, dissolved oxygen condition, sediment deposition, and habitat availability. Early life stages, particularly eggs and larvae, appear particularly susceptible to the adverse impacts of flow, since they have a limited capacity for behavioural responses to altered flow conditions. A constraint to conservation and management efforts for salmonids is in selecting river flow targets at the catchment scale with confidence. Most studies linking flow with salmonid population processes are site specific, and may not be readily transferable to other sites. Despite this uncertainty, the requirement for catchment level flow targets has become critical as pressure on water resources has intensified, at the same time that salmonid populations have declined.

INTRODUCTION

In this chapter I review the current literature on the effects of flow on salmonid fishes. River flow regimes influence a number of key aquatic processes, including levels of dissolved oxygen, sediment transport and deposition, water quality (through dilution and flushing), and habitat type and distribution (Poff et al., 1997; Richter et al., 1998; Bunn and Arthington, 2002). These processes influence the distribution and abundance of biota and flow regimes can thereby directly or indirectly, determine the spatial and temporal distribution of fish (Jowett et al., 2005; Poff and Zimmerman, 2010). Human perturbation of flow, either by directly extracting water, regulating rivers using weirs and dams, or indirectly through patterns of land use, may affect fish populations and communities (Freeman et al., 2001; Cattanéo, 2005; Park et al., 2006; Benejam et al., 2010). Understanding the relationship between flow and fish abundance and distribution represents a key goal in aquatic ecology and fisheries management, and particularly in attempts to manage, restore and rehabilitate rivers for the benefit of aquatic communities (Richter et al., 2003; Souchon et al., 2008; Poff et al., 2010). Because of their ecological and commercial importance, salmonids have been the chief focus of the debate over flow management (Quinn, 2011; Milner et al., 2012).

In recognising the dominant role of river flow on salmonids an additional consideration is the life-stages affected (Nislow and Armstrong, 2012). The direct and indirect effects of river flow will affect different salmonid life-stages in distinct and sometimes contrasting ways (Johnson et al., 1995; Malcolm et al., 2012; Milner et al., 1998; Nislow and Armstrong, 2012). The impacts of flow that act strongly on developing eggs (Steen and Quinn, 1999) may differ from those impinging on, for example, juveniles (Elliott et al., 1997) or migrating adults (Solomon and Sambrook,

2004). Impacts on different life-stages will depend on the timing and duration of low or high flow events (Bischoff and Wolter, 2001). High flows may have a profound effect on early life stages, whereas periods of low flow may interrupt the migration of adults. The flow requirements of salmonids have been reviewed exhaustively (Quinn, 2011; Nislow and Armstrong, 2012) and are not repeated here.

The significance of flow for salmonids

The aim of this review is to summarise key scientific studies that demonstrate how river flow can influence the abundance of salmonid fishes, though where relevant, case studies using non-salmonid taxa are also included. A secondary goal is to identify which aspects of flow play the most significant role in shaping salmonid populations, and thereby, how this information might be used in river management, and rehabilitation and restoration of rivers for salmonids. The review focuses on salmonids because the bulk of studies that have addressed this question have concentrated on this family of fishes, a reflection of their economic and perceived ecological importance. Many salmonids are also of considerable conservation interest (Allendorf and Waples, 1996). Migratory salmonids occupy entire river catchments, from headwaters to estuaries, with each life stage having some dependency on different habitat types making them particularly sensitive to river flow regime alteration. Salmonids have, consequently, been considered good ecological indicators of the impact of flow regime on ecosystems over a broad range of environmental scales (Milner et al., 2012).

Another feature of salmonid biology that makes them a valuable model in understanding the ecological impact of flow is the plasticity of their life-history traits in response to environmental variability (Klemetsen et al., 2003; Rieman and Dunham,

2000). Thus salmonids display wide intra- and interspecific variability in responses to flow variability, with the capacity to adapt to high-gradient upland streams and lowland rivers and estuaries (Beechie et al., 2006; Moore et al., 2012). While this feature of salmonid biology can serve to identify how flow regimes select for specific life-history traits, these adaptive responses also make it difficult to derive generic models of the impacts of flow, with potentially contrasting results generated in different locations (Milner et al., 2012).

Describing river flow

Hydrologists typically use the term 'flow' to describe the volume of water that is discharged past a single point on a river. The flow regime of a river comprises flow magnitude, frequency, duration, timing and rate of change (Poff et al., 1997). Various numerical variables are used to describe mean, median, peak and low flow rates so that each of these components of water flow can be estimated (Poff et al., 1997; Shaw, 1988). Originally these descriptors were intended for river engineering or water resources management, driven by human population needs, such as flood alleviation or public water supply (Newson, 1994). Regulatory changes over time have shifted the emphasis of river and water resources management towards an ecological basis in order to meet the requirements of legislation, such as the EU Habitats Directive (European Commission, 1992) and the EU Water Framework Directive (European Commission, 2000). Consequently, the term 'environmental flow' has entered usage to denote the amount of flow required in a watercourse to maintain a healthy ecological state (Arthington et al., 2003; Gibbins et al., 2001; Acreman et al., 2008). The introduction of this term is problematic since quantifying 'environmental flow' is difficult for complex

ecological systems, though it at least encapsulates an important concept. Despite these difficulties environmental flows are widely used to set abstraction limits and reservoir releases in river management and are typically defined in terms of departure from some baseline state, such as the 'natural' flow, itself a subjective concept since natural flows will change periodically in response to seasonal and climatic variation (for a full discussion see Poff et al., 1997). If the science and application of environmental flows is to develop, a better quantitative understanding of flow variability and biological response is required (Poff et al., 1997). For this review my goal was to evaluate the evidence for flow-induced responses in salmonids, and to identify the key aspects of those responses that appear relevant to the setting of environmental flows for salmonid management and as targets for restoration measures. For a recent review of terminology see Milner et al. (2011).

Part of this chapter outlines the processes that drive river flow so that their different scales and interactions can be placed in context when considering biological responses. This conceptual background is important to those with biological or ecological training in order to gain better insight into the hydrological disciplines that tend to dominate river and water resources management. Transference can then be made to the rehabilitation of river ecology and restoration of natural features in engineered or degraded rivers. For brevity I employ the term 'restoration' to denote both river rehabilitation and restoration measures.

DETERMINANTS OF RIVER FLOW

The natural flow regimes of rivers can vary markedly depending on the sources and components of water runoff. Freeze (1972) partitioned the total runoff from a natural

catchment into four component parts: channel precipitation, overland flow, interflow (subsurface flow), and groundwater flow (Freeze, 1972; Ward, 1974). Channel precipitation is that which falls directly onto the river water surface and represents the smallest component, since river surface area will make up only a small percentage of total catchment area. Overland flow is runoff that fails to infiltrate the substrate surface and is determined by the degree of soil saturation. Interflow occurs when water infiltrates the soil and moves laterally through the upper soil horizons to reach river channels. Precipitation that percolates through soils to the underlying water-bearing strata contributes to the groundwater flow component. Groundwater flow tends to lag behind rainfall events and is important in sustaining river flow during periods of little or no rain. The relative contribution of each of these components will determine the flow regime of a river. When these components are considered alongside other catchment characteristics, such as catchment size, rainfall pattern (spatial and temporal), geology, soil type and topography, an extensive range of river flow regimes will result (Ward, 1974; Newson, 1994; Poff et al., 1997). For example, upland rivers in northern Europe have a high runoff per unit area due to high rainfall and low evapotranspiration, combined with an impermeable geology, steep gradients and thin soils (Burt, 1992; Gilvear et al., 2002). They generally show marked flow peaks and troughs in response to periods of high and low rainfall due to short lag times between rainfall events and changes in river flow (Shaw, 1988). In contrast, lowland alluvial rivers will be influenced more by groundwater. As such, these show relatively more consistent and stable patterns of flow due to a damped response to rainfall and sustained flows in dry periods (Shaw, 1988). A further contrast is found in regions, such as North America, that experience significant precipitation in the form of snow, where river flow can be

dominated by patterns of snowmelt. An assumption is that these varying patterns of flow will select for contrasting salmonid life histories, an assumption that appears to be justified (e.g. Elliott, 1995; Beechie et al., 2006).

Approaches to understanding river flow regime need to reflect regional patterns. In the UK, the Institute of Hydrology developed the Base Flow Index (BFI) as a standard approach to apportioning the total river outflow to base flow (Newson, 1994). The highest BFI scores relate to chalk and other porous limestone catchments, whilst the lowest corresponds to clay-dominated catchments. This index provides hydrologists and water resource managers with a comparative guide to identify catchment types that are likely to be prone to low-flow conditions. In the USA, Reidy Liermann et al. (2012) developed a system of classification of rivers with relevance for the Pacific Northwest. Using a Bayesian mixture model they identified seven major classes of flow, a critical first step for setting flow requirements in the region. At a broader scale, Poff (1996) used the hydrological characteristics of relatively undisturbed rivers across continental USA to derive a river classification scheme that reflected patterns of flow variability among rivers. Attempts at a comparable hydromorphological assessment of European rivers have been less comprehensive (e.g. Raven et al., 2002; Downs and Gregory, 2014), though the EU Water Framework Directive now requires a status assessment of all water bodies.

GEOMORPHOLOGY

River flow patterns are dependent on the nature of the catchment through which they flow, which in turn is dictated by the underlying geology and topography and ultimately rainfall, the primary determinant of flow patterns (Helliwell et al., 2007). However,

despite having similar controls, in terms of hydrology and geomorphology, river flow patterns may still diverge (Schumm, 1985). In addition to pattern diversity, Schumm (1985) noted that rivers also exhibit variation in their stability and resistance to erosion, stemming from differences in bank and bed material and hydrological regimes. Nevertheless, the same controls operate at all scales from catchment and whole river at the broadest scale, to river reach at the medium scale, through to small-scale processes such as in-channel features and sediment structure (Schumm, 1985; Newson and Newson, 2000). Geomorphological processes define both channel form and the controls on channel form, which ultimately determine channel change (Environment Agency, 1998). The interaction of flow with geomorphology, lithology and valley form are important elements in determining the physical habitat experienced by the biota living within a river (Poff et al., 1997; Newson and Newson, 2000), in particular determining bed scour depth, water velocity and depth, and inter-gravel flow for spawning salmonids and their eggs (Boughton et al., 2009).

NATURAL CONSTRAINTS ON RIVER FLOW

The four main runoff components to river flow (channel precipitation, overland flow, interflow and groundwater flow) are controlled through variations in climatic and catchment factors and their interaction (Ward, 1974; Shaw, 1988; Briggs et al., 1997). These controls are generic in that they influence both high and low river flow through their differing temporal and spatial variation and the nature of the interactions (**Figure 1**). Low river flows are natural phenomena that are ultimately dependent on a lack of rainfall and limited groundwater inputs. The main processes that sustain river flows in dry weather are storage and discharge from within the catchment consisting of

groundwater and subsurface flow, storage in wetlands, lakes or snowmelt (Smakhtin, 2001). Patterns of low flows are determined by temporal variation in the magnitude of low flows, its variability, flow depletion and duration, along with spatial variations due to the regional distribution of rainfall, channel morphology, drainage network and catchment altitude and topography (Shaw, 1988; Briggs et al., 1997; Smakhtin, 2001). In general terms, rivers in catchments with permeable geologies have a greater capacity to sustain river flows than rivers in impermeable catchments.

The processes that determine low flow conditions are similar to those that determine flood flow conditions (**Figure 1**). Again, variation in meteorological and terrestrial components will influence flooding seasonality, frequency, duration and intensity (Ward, 1974; Briggs et al., 1997). Flooding tends to have a seasonal pattern, for example, in northern Britain the majority of flood events (>78%) occur in the winter period between October to March, though they have been recorded at all times of year (Black and Werrity, 1997). Although flooding can be seasonal, flood conditions can also occur unpredictably and develop more quickly than low flow conditions, so can be seen as exerting greater influence on riverine communities (Junk et al., 1989; Poff et al., 1997).

ANTHROPOGENIC EFFECTS ON RIVER FLOW

Globally there are few riverine systems whose flow regime is unaffected by human activities (Ward, 1974; Petts, 1984; Sala et al., 2000). A range of human activities is capable of affecting rivers both through direct alteration of river channel habitats or through changes to hydrological and geomorphological processes, which ultimately alter river flow regimes (Poff and Allen, 1995). Dams and other hydraulic structures,

agricultural and forestry practices, urbanization and water abstraction have the potential to alter river flow regimes and impact on river biota, including salmonid populations.

Water abstraction and impoundments

Impoundments and abstractions can lead to reduced annual and seasonal flow volumes. Groundwater abstractions can reduce the base flow of rivers that depend upon this component of runoff to sustain flows during periods of low rainfall (Strevens, 1999; Weber and Perry, 2006). Additionally, headwater streams in high base flow catchments can dry up, or their sources migrate downstream, thereby reducing habitat availability for fish and other organisms. The reduction of groundwater flow into rivers can also lead to thermal impacts on biota (Caissie, 2006). Salmonids have relatively exacting thermal requirements (Elliott, 1995; Wootton, 1998), with impacts on survival, growth, movement, migration and emergence (Caissie, 2006). In chalk streams in the southern UK, the reduction of relatively cool groundwater is recognised as a potential limiting factor for the survival of salmonids, especially when air and water temperatures are elevated (Solomon and Lightfoot, 2008). Similarly, rainbow trout (*Oncorhynchus mykiss*) in streams in Oregon, USA were dependent on cold water refugia created by upwelling groundwater to persist in warmer stream reaches (Ebersole et al., 2001).

Surface water abstraction can also reduce flow over a range of scales, from annual to daily, especially where large public water supply intakes are in operation. Large water intakes or diversions can disrupt the attractant flow for salmonids during downstream migration, leading to the entrapment of individuals and removal of significant numbers from the spawning population (Solomon, 1992; Aprahamian and Jones, 1997; Turnpenny et al., 1998). Other surface water intakes, for practices such as

fish farming and watercress cultivation, tend not to affect the overall water resource budget as they return nearly all the water they use, though they can create river reaches that are depleted of flow and thus present habitat loss and potential barriers to migration for fish (Jones, 1990; Casey and Smith, 1994; Kelly and Karpinski, 1994). Fish farms can also degrade water quality and introduce pathogens to wild fish (Crisp, 1993). Reservoir operations can extensively modify the flow regime of rivers downstream, tending to reduce flow variability and aspects of the flow regime that play a role for specific life history stages (Gustard et al., 1987; Magilligan and Nislow, 2001; Pavlov et al., 2008). For example, flows that would normally transport fine sediment downstream, helping maintain hydromorphological conditions for biota, can be removed resulting in reduced sedimentation of river reaches below the dam. An outcome is coarsening of the substrate, termed 'bed armouring', which limits habitat availability, as well as increasing the risk of 'downcut' or channel erosion (Poff et al., 1997; Pulg et al., 2013; Osmundson et al., 2002). Natural low flow conditions can also be elevated by reservoir compensation flows, which may have been set without any ecological basis (Gustard et al., 1987; Acreman and Dunbar, 2004). Low flows may be needed during the period of emergence of larval salmonids to prevent washout and promote growth (Humphries and Lake, 2000).

Hydropeaking

Flow regulation and management for activities such as hydropower present fish downstream of the point of water release with a strikingly unnatural environment in terms of flow regime. The rapid increase in flows from dam releases (hydropeaking) are non-seasonal, frequent, of high magnitude and have varied duration (Lucas and Baras,

2001). Water released from dams may be at a lower or higher temperature than the river into which they are released. In some cases released water may be depleted in oxygen, in other cases supersaturated (Lucas and Baras, 2001).

The impact of hydropeaking may vary among species and river types. Scruton et al. (2003) detected species-specific behavioural responses in salmonids. Atlantic salmon (*Salmo salar)* showed two distinct patterns during hydropeaking trials, fish either showed high site fidelity or moved substantial distances in response to water releases. In contrast, brook trout (*Salvelinus fontinalis*) moved more in relation to releases than to stable flows and also moved more at night in both stable and dynamic flow conditions. Valdez et al. (2001) investigated the effects of dam releases on the Colorado River and found little effect on the distribution, abundance or movement of native fish, proposing that the magnitude and duration of releases were insufficient to displace populations on this river. Hydropeaking has also been associated with strandings, with sudden reductions in flow leaving fish isolated in pools or on exposed substrate (Saltveit et al., 2001; Irvine et al., 2009).

Flood risk management

Mitigating flood risk is a major, though not exclusive, source of river engineering works (Smith and Winkley, 1996; Petts, 2009). Flood risk measures typically involve the straightening and resectioning of river channels to increase conveyance, and gravel removal to lower the riverbed and thereby increase channel capacity (Purseglove, 1988). Impediments to flow are also removed. Thus, boulders and woody debris are removed from the river channel, and riparian vegetation is cut back or removed altogether (Brookes et al., 1983; Harmon et al., 1986). Channelisation and river clearance generate

structurally simple and hydraulically efficient river channels that facilitate the rapid clearance of water from the floodplain (Brookes, 1985; Hodgson and O'Hara, 1994). These measures have the effect of intensifying the impact of high flows (Poff et al., 1997; Petts, 2009). In addition, the loss of structural complexity and refuge habitats through river modification serve to exacerbate the impact of high flows on fish. Loss of connectivity with the floodplain in particular has the effect of impeding access to low flow conditions, which may be critical spawning habitat or for early life stages (Junk et al., 1989; Poff et al., 1997). The overall impact of flood mitigation activities also tends to alter the ecological function of a river and thereby on the fish populations inhabiting it (FAO, 1984; Poff et al., 1997; Pretty et al., 2003).

Land use

Riparian land use can influence river flow, primarily through modifying rates of runoff and introducing sediment. A study by Allan et al. (1997) demonstrated that while catchment level patterns of land use predicted runoff and sediment input, local scale land use was uncorrelated. Scale effects of land use have prompted a 'riverscape' approach to management, particularly of salmonids, but also of other fish taxa (Fausch et al., 2002). This approach recognises that different physical processes that control river flow operate at different spatial scales (**Figure 2**).

DIRECT EFFECTS OF FLOW ON FISH

River flow, either high or low, may have an impact on fish directly and may be felt differently at different life-stages (Nislow and Armstrong, 2012). Seasonally high flows and flooding are a dynamic but natural aspect of the character of a river's flow regime

and play a critical role in determining the ecological integrity and biological productivity of rivers (Junk et al., 1989; Poff et al., 1997). Periods of low river flow are also natural and often strongly seasonal phenomena that create conditions in the river channel strikingly different to those under high flows. The proportion of high velocity and associated high energy areas are dramatically reduced during periods of low flow, and water depth in these areas tends to be shallow; conditions likely to have an effect directly on the movements and activities of fish (Solomon and Sambrook, 2004; Wissmar and Craig, 2004; Tetzlaff et al., 2008).

Biotic adaptations to flow

River biota exhibit adaptations to the natural heterogeneity of river systems and many organisms show adaptive resilience to a wide range of flows for example through morphological adaptations (suckers, claws or other mechanisms for holding fast in high flow), reproductive strategies (releasing eggs at particular flow events) and tactics to escape in space and time (migrating to specific locations during particular flow periods) (Lehtinen and Layzer, 1988; Southwood, 1988; Townsend and Hildrew, 1994; Vogel, 1994). Flood events may also have the effect of limiting the establishment of invasive species that lack adaptations for high flow conditions (Valdez et al., 2001). A negative impact on fish assemblages may occur when human activity modifies the pattern of river flow so that it deviates from its natural range (Petts, 2009). Human activity can alter variation in flow such that the frequency and duration of flood and drought events may be prolonged. In other circumstances, such as downstream of reservoirs, they may be eliminated altogether.

Effects of high flows

Fish production and growth may be linked to the extent of accessible floodplain (Junk et al., 1989), and nutrient inputs to rivers can be facilitated by high flows flushing adjacent floodplains during periods of high water discharge, thereby enhancing fish productivity (Bowes et al., 2005). In some taxa, spawning is directly related to flood cycles, enhancing reproductive success by creating spawning habitat and nursery areas (Wootton and Smith, 2015). However, the type of river channel and its location within a catchment can determine how floods drive productivity and biotic interactions. Low order streams may experience short and unpredictable flood events, with fish and other aquatic organisms having limited adaptations for using the aquatic/terrestrial transitional zone. Conversely more natural channels or higher order streams have a more predictable and longer flood pulse, with aquatic organisms showing adaptive strategies for utilizing the 'aquatic-terrestrial transition zone' (Junk et al., 1989). Highly modified channels often preclude access to the transition zone. Fish that occupy rivers with prolonged and predictable floods often show adaptations to exploit the presence of seasonal floods and exhibit life history strategies that maximize their reproductive fitness (Langler and Smith, 2001; Zeug and Winemiller, 2008). Nevertheless, the seasonal timing, magnitude, duration and frequency of flood events will have different effects on the key life stages of fishes (eggs, larvae, juveniles and adult) (Wolter and Sukhodolov, 2008; Poff and Zimmerman, 2010; Konečná et al., 2009), and these are considered separately.

Fish in the early life stages (unhatched egg, embryo and larvae) have a limited capacity actively to seek out preferred habitats and so depend upon drift to transport them to an optimum environment that maximizes their rate of growth and development, and survival (Wolter and Sukhodolov, 2008). However, the timing of drift and the

magnitude of displacement will have different optima among species (Reichard and Jurajda, 2007; Pavlov et al., 2008). Unusually large and un-seasonal floods may be detrimental to fish populations by transporting early life stages downstream away from optimum habitat (termed 'washout') or outside the river channel altogether (Fausch et al., 2001; Wolter and Sukhodolov, 2008). Conversely, the absence of natural periodic floods may fail to redistribute early life stages leading to elevated densities and competition (Zitek et al., 2004; Reichard and Jurajda, 2007). In some cases flood events may enable early stages to reach floodplain refugia, such as ponds, lakes or ditch systems necessary for them to complete development and/or avoid predation (Seddell et al., 1990; Tockner et al., 2000). In other cases flooding may enable young fishes to migrate down river and recruit to the adult population (Halls and Welcomme, 2004).

The early life stages of salmonids appear susceptible to major floods, despite a widespread view that their preferred river types are relatively high flow velocity environments compared with other freshwater fishes (Sukhodolov et al., 2009). During reproduction their eggs are deposited at an optimum depth in river gravels to minimize the risk of wash out, but sufficiently shallow to ensure adequate oxygenation for egg development and permit larval emergence (Crisp, 1989; Crisp and Carling, 1989). However, extreme floods that mobilize the substrate can damage eggs (Jensen and Johnsen, 1999), although such floods are relatively rare events. The impact of more regular spates are largely mitigated by the depth of egg deposition (Crisp, 1989) and composition and stability of spawning sites, termed 'redds' (Beard and Carline, 1991). Nevertheless, a degree of high flow is needed to promote flushing of fine sediment from gravels to maximize oxygen supply to eggs and embryos (O'Connor and Andrew, 1998; Jensen and Johnson, 1999; Levasseur et al., 2006), although if sediment input exceeds

the transport and flushing capability of the river then gravel siltation is inevitable (O'Connor and Andrew, 1998). In addition to oxygen stress on eggs, fine sediment has the capability to entomb embryos and prevent emergence (O'Connor and Andrew, 1998; Jensen and Johnson, 1999). The emergence phase is seen as a critical one, with strong density-dependent mortality at this stage, but density-independent factors, such as flooding, can also increase mortality substantially (Elliott, 2006). An adaptation to compensate for the negative effect of floods is that emergence is timed to coincide with a low probability of flooding (Fausch et al., 2001; Elliott, 2006; Lobon-Cervia, 2009). Experimental studies have shown that newly emerged salmonids are most sensitive to wash out, though their susceptibility declines over time, corresponding with an increase in body size and swimming ability (Heggenes and Traaen, 1988).

Post-larval juveniles and adults possess an enhanced capacity to navigate their way to preferred habitats, and to seek out refuges during peak flows (Wolter and Sukhodolov, 2008). This capacity suggests that the impact of flooding is likely to be felt less strongly at these stages, though the duration and magnitude of flooding will determine the impact, with unseasonal and exceptionally high flood events expected to have greatest impact. Jurajda et al. (2006) detected only minor effects on a cyprinid fish assemblage, and no significant change in fish density, in a tributary of the River Danube, immediately before and after exceptional summer floods during which river discharge peaked at 2000% of the long-term mean. Similarly, the displacement of barbel (*Barbus barbus*) by high summer flows in a UK river was followed by the fish homing back upstream to their former resident areas (Lucas, 2000). Notably, autumn displacement was more frequent and homing less frequent, suggesting a seasonal element to the effects of displacement (Lucas, 2000).

However, in some cases severe flood events have the potential to drastically reduce fish populations and increase the risk of local extinction. Sato (2009) measured dramatic declines (*c*. 98%) in a population of Japanese white spotted char (S*alvelinus leucomaenis*) inhabiting mountain streams following a severe flood, with no sign of recovery two years after the event. In this case, flood flows were so severe that bank-side debris were mobilized, which had the impact of largely eliminating fish at a local scale and significantly changing the structure of the environment. This study highlights how isolated fish populations in lower order upland streams may be at greater risk of extinction from catastrophic flood events because fish are unable to move readily out of the main river channel in the way they often can in unregulated lowland rivers, and goes some way to supporting the 'flood-pulse' concept (Junk et al., 1989). The flood-pulse concept posits that rivers and their floodplains comprise a single ecological and hydrological system with correlated responses to pulses in river discharge. Observations on stream-living marble trout (*Salmo marmoratus*) populations have revealed reductions of between 31% and 78% following severe flood events prior to spawning, but without long-term consequences to the population. The quick recovery of populations was possible because of a high intrinsic rate of population increase for this species, allowing the small number of reproductive individuals that survived a severe flood to successfully re-establish local populations (Vincenzi et al., 2008). Studies suggest that salmonid reproductive strategies show compensatory responses for dealing with extreme flows, at least within certain limits, which buffer negative effects at the population level.

Effects of low flows

In low flow conditions the overall volume of water in the river is substantially decreased, with a concomitant reduction in average depth and width of the river channel, which in turn will result in a net reduction in available habitat. This situation may present fish with the problem of obtaining access to preferred habitats for feeding, and the risk of oxygen stress.

When flow falls to the point that the risk of stranding or isolation become a serious threat fish rely on refugia habitat for survival until flow conditions improve. Refugia include areas of deeper water (Huntingford et al., 1999; Armstrong et al., 2003), which may include disconnected pools (Labbe and Fausch, 2000; Magoulick and Kobza, 2003). Davey and Kelly (2007) found refugia to be critical in enabling brown trout (*Salmo trutta*) to persist in a river with naturally intermittent flow in its middle reaches. They showed that brown trout (and other species) moved upstream as the stream dried, with sections subject to drying only slowly recolonized. Rates of colonization correlated negatively with increasing distance to refugia and the fish assemblage in sections susceptible to drying were quantitatively and qualitatively different to neighbouring reaches. Davey and Kelly's (2007) findings suggest that river systems can exhibit similar ecological processes predicted from island biogeography theory (MacArthur and Wilson, 1967), with habitat colonization rates negatively correlated with distance from the source of colonizers. From an applied viewpoint this finding has implications for the way habitat quality and its connectivity along river corridors should be viewed and managed.

Intermittent rivers, those that only flow for some part of the year, are potentially important habitat for juvenile salmonids. In the western USA, intermittent rivers

comprise over 65% of total river length and are a source of both spawning and nursery habitat. In a study of coho salmon (*Oncorhynchus kisutch*), Wigington et al. (2006) showed intermittent rivers to be key sites for the production of smolts, with juveniles able to persist in isolated pools between periods when river flow ceased.

In the case of predictable seasonal reductions in flow, fish may show adaptations that enable them to respond to the changed conditions, including dispersal (Pires et al., 1999). However, in many cases dispersal may be limited if there is too little water due to channel constriction (Crisp, 1989; Armstrong et al., 2003). Under the most extreme low flow conditions a river may comprise nothing more than a series of isolated pools. However, even if the river continues to flow as a discrete water body, the appearance of barriers such as gravel banks and boulders, that would be otherwise submerged, may impede fish movement.

A consequence of reduced low flows, then, will be elevated fish density, particularly if fish are unable to redistribute themselves. At a high density fish may face a greater risk of hypoxia and possibly predation, including cannibalism (Smith and Reay, 1991). In addition, a number of population processes are density-dependent. Thus, feeding and growth may be limited, while mortality rates would tend to increase. The transmission of pathogens is often strongly contingent on host density, especially if transmission is direct. In species that show territoriality or dominance hierarchies, which is frequently the case in salmonids, injuries and mortalities associated with aggression may also increase. The negative effects of low flow will depend on the extent of flow limitation, and also the period over which low flows occur. Elliott et al. (1997) noted that a juvenile year class of brown trout subjected to successive drought periods had lower growth rates and increased mortality, which was strongly linked to

reduced densities of returning females. Summer droughts may not affect survival as much as low rainfall in spring and summer, or in summer and autumn, when low stream flows can be prolonged. The effects of low flow may also interact with other variables, notably temperature. Solomon and Lightfoot (2010) found correlations between poor salmon stock performance and reduced August flows, possibly linked to temperature effects on spawning migration. High water temperatures will exacerbate hypoxic effects resulting from low flow (Milner et al., 2003), while low winter flows may increase the risk of fish kills from freezing (Huusko et al., 2007). Notably Sabaton et al. (2008) demonstrated increases in the abundance of adult and juvenile brown trout when flows were restored to streams. Although increases in flow were not large, weighted usable area; i.e. available physical habitat, increased substantially in some rivers, suggesting that the impacts of low flow, and attempts to restore flow to rivers, are likely to be highly variable among rivers.

The negative impacts of low flow on fish may be especially damaging at the population level if they occur during periods of reproduction. Young stages have a limited capacity to avoid stranding, hypoxia or withstand periods of restricted ration (Wootton, 1998). However, the hyporheic zone may be utilised by the eggs and larvae of some species, and may not be unduly affected by low flows (Baxter and Hauer, 2000), though the risk to salmonids from egg desiccation can be considerable (Crisp et al., 1984; Milner et al., 2003). Furthermore, droughts have been identified as a main cause of severe reductions in the number of young-of-year (YoY) salmonids with impacts on population size (Bell et al., 2000; Lobon-Cervia, 2009). These studies also demonstrate the resilience of populations where suitable in-channel habitat exists.

Effects of variable flow

While low and high flow rates can have an impact on salmonids, especially if these are of unusual magnitude or are unseasonal, another little understood impact is through increased variability in flow. Evidence from rivers subjected to pulsed water releases associated with hydropower generation (termed 'hydropeaking', see above) suggest that highly variable flows have negative effects on salmonids, especially on young stages. For example, Freeman et al. (2001) showed that high flow variability had a negative effect on juvenile fish by undermining habitat persistence. In a study of stream fish assemblages, Poff and Allan (1995) showed that the effect of a high coefficient of variation of flows generated fish communities distinct from those with low flow variation.

Even modest changes in the pattern of flow can alter the behaviour of territorial juvenile salmonids quite substantially. Juvenile salmonids usually rest on the substrate facing upstream under low flow conditions at a specific 'station'. From this point they collect food items that drift along the riverbed or in the water column and engage in aggressive behaviour with neighbouring territory holders (Jonsson and Jonsson, 2011). As flow increases they leave the substrate and swim more frequently in the water column. Here they can see and encounter neighbours more frequently, with a result that territory size increases, with a concomitant reduction in fish density (Kalleberg, 1958; Keenleyside, 1962).

In contrast, Heggenes et al. (2007) observed no difference in the home range size of brown trout between channelised and natural river sections, and no consistent effects of abrupt changes in flow. The direct effects of flow on fish probably depend on local hydrological conditions, with optimal flows likely to be different in different

sections of a catchment. Rosenfeld et al. (2007) proposed that habitat suitability for rainbow trout based on hydraulic geometry changed longitudinally along a river. Thus, optimal conditions for juvenile stages were predicted for smaller upstream sections, while those for larger fish were found downstream. These predicted patterns matched empirical data. A summary of stage-specific responses to flow variability is presented in **Table 1**.

INDIRECT EFFECTS OF FLOW ON FISH

River morphology

River and water resource management tends to focus solely on the direct impacts of flow (Petts, 2009). However, flow is often simply a surrogate for a more complex interaction between channel morphology, water depth and flow that underpins the availability of habitat for river biota (Brooker and Graynoth, 2008). Changes to river flow regime can result in changes to both habitat quantity and quality at a range of scales. Because fish migrate among different 'meso' and 'micro' scale habitats there is potential for effects of flow at the population level (Pavlov et al., 2008). Consequently, an understanding of the role of river morphology during different salmonid life stages is important if flow effects are to be understood. Experimental addition and removal of boulders in the Little Southwest Miramichi River by Dolinsek et al. (2007) showed that the presence of boulders significantly increased juvenile Atlantic salmon (*S. salar*) density, though not of non-salmonid species. The presence of coarse woody debris has also been shown to have a positive effect on juvenile salmonids, primarily by diversifying flow conditions and thereby enhancing feeding opportunities and providing

refuges from high flow conditions (Harmon et al., 1986; Roni et al., 2008; Hafs et al., 2014).

Temperature

The energy budgets of fish are driven strongly by water temperature (Rankin and Jensen, 1993; Wootton, 1998), which is negatively correlated with flow rate (e.g. Webb et al., 2003). Therefore there are potential consequences of reduced or enhanced flow rates for fish bioenergetics, and ultimately on the survival of certain life stages indirectly through their effect on water temperature (Wootton, 1998). Water temperature also plays a major role in controlling the upstream migration of some salmonids (Quinn et al., 2007; Moore et al., 2012).

Sediment

The rate of transport of sediment is a function of flow, with the greatest volumes of material transported during flood events (Walling and Webb, 1992; Kondolf, 1997; Lenzi and Marchi, 2000). Land management activities, particularly agriculture but also forestry, mining, road construction, effluent discharge, and urban sources, can all result in elevated sediment inputs to watersheds (Henley et al., 2000; Walling and Webb, 1992). Sediment inputs are not wholly rainfall dependent, and so can occur when their impact may be most ecologically damaging (Marks and Rutt, 1997), though rainfall will ultimately determine the rate and volume of sediment transport into and along the river channel. Catchment and river type can also influence sediment transport and deposition processes (Lenzi and Marchi, 2000).

Increased sedimentation and turbidity leads to decreased primary production that can cascade through trophic levels (Osmundson et al., 2002). The avoidance of turbid waters has been observed in juvenile coho salmon, arctic grayling (*Thymallus arcticus*), and rainbow trout (Newcombe and Jensen, 1996). The negative effects of suspended particles have been observed on juvenile and adult stages in fishes through gill damage (Berg and Northcote, 1985), and reduced feeding rates (Waters, 1995; Argent and Flebbe, 1999). Perhaps, the biggest impact on salmonid production, though, is likely to come from sedimentation affecting oxygen supply and uptake by eggs (**Table 2**). A meta-analysis of the impact of sediment on egg to juvenile survival in four species of Pacific salmon by Jensen et al. (2009) showed coho salmon to be most vulnerable and chum salmon least susceptible, while Chinook salmon and migratory rainbow trout showed intermediate sensitivity.

While the transport of large amounts of sediment resulting in fine sediment intrusion is associated with moderate to high flows (Wood and Armitage, 1997), low winter flows at times of low rainfall and icy conditions, can also result in the infiltration of sediment into spawning redds (Levasseur et al., 2006). A consequence is that natural sediment inputs that occur during high flow events can result in less severe ecological effects than at times of low flow (Marks and Rutt, 1997). Hence, although periods of high rainfall increase the input of sediment to a river, the effects can be partly be mitigated by dilution and mobilization of sediment under high flow conditions while, counter intuitively, low flow conditions can result in siltation of the river channel (Wood and Armitage, 1997).

Dams have the effect of removing all but the finest suspended sediment, resulting in sediment-depleted water. A common outcome is increased coarsening or

'armouring' of the riverbed, which can limit habitat availability for aquatic invertebrates on which juvenile salmonids feed. Loss of coarse sediment also creates a riverbed that may be unsuitable for spawning by adults (Poff et al., 1997).

Oxygen

Well-oxygenated water is important for all salmonid life stages (Armstrong et al., 2003; Hendry et al., 2003). Oxygen availability is especially important during egg development, since at this life stage the fish are unable to show a behavioural response to low levels of dissolved oxygen. Fine sediments have multiple impacts on the supply of oxygenated water to developing salmonid eggs and alevins (Crisp, 1996; Grieg et al., 2005a). Fine sediments can limit interstitial flow velocities, while organic sediment has the effect of depleting dissolved oxygen levels (O'Connor and Andrew, 1998; Acornley and Sear, 1999; Grieg et al., 2005a). Clay particles create low permeability seals on the surface of salmonid eggs, greatly reducing rates of oxygen consumption (Grieg et al., 2005b).

Dissolved oxygen concentration and water flow are often correlated, and the relationship between flow and dissolved oxygen availability often confounds links between flow and other variables (Downes, 2010). Low summer flows and elevated temperatures in rivers are associated with reductions in dissolved oxygen concentration. These effects occur through reduced oxygen solubility and an elevation in oxygen consuming metabolic processes at higher temperatures. At low flow rates water turbulence is also reduced, which limits re-aeration of oxygen-depleted water. Fish growth and activity increase with a rise in temperature to an optimum, at which point they become increasingly constrained by oxygen availability (Jonsson and Jonsson,

2009). Reduced oxygen levels can also lead to greater susceptibility to disease (Johnson et al., 2009), and to a reduction in migration into freshwater by salmonids (Solomon and Sambrook, 2004).

Pollutants, nutrients, BOD

Water quality can be a limiting variable for salmonid population productivity. Efforts to rehabilitate rivers for salmonids and other fishes may not be fully realized if water quality is limiting (Ormerod, 2003). River flow exerts an effect on water chemistry through a dilution effect (Webb and Walling, 1992). High flow rates may also mitigate the anoxic effects of organic pollutants. Reduced flow conditions tend to exacerbate the impacts of pollutants (Smakhtin, 2001), which can be further aggravated at elevated water temperatures when pollutants tend to have greater toxicity (Alabaster and Lloyd, 1982; Mason, 2002). Episodic pollution events without adequate dilution, during periods of limited flow, have the greatest impact and can lead to ecosystem degradation (McCahon and Pascoe, 1990).

Aquatic and riparian vegetation

Indirect impacts of river flow on salmonids can come through effects on other components of the river community, particularly instream and riparian vegetation. Instream, but particularly riparian tree cover, is important in providing shade and thereby plays a role in water temperature regulation (Eklöv et al., 1999). Vegetation can additionally enhance the production of macroinvertebrates (Robinson at al., 2002; Gowan and Fausch, 2002), an important food supply for salmonids that can determine their local distribution (Kawaguchi and Nakano, 2001). Coarse woody debris is

recognised as an important component of habitat structure. It functions by regulating sediment transport, effects debris and sediment accumulation, and dissipates energy by impeding flow and providing refuges for fish and invertebrates (Van Kirk and Benjamin, 2001).

Productivity and bioenergetics

Rate and variance of river flow can influence rate of food delivery to salmonids, primarily in the form of drifting invertebrates that are of either terrestrial or aquatic origin (Kawaguchi and Nakano, 2001). The energetic costs of holding station in a river to feed influences fish energy expenditure, as does water temperature, thus the impact of flow can influence salmonids through the structure and balance of their energy budgets. Field studies with salmonids have shown that those in fast currents attain higher food consumption rates than those in slower currents but experience lower growth rates through greater energy expenditure (Tucker and Rasmussen, 1999).

MANAGING RIVER FLOW

Directly or indirectly river flow can influence different aspects of salmonid life cycles, as well as being important to other river biota. Other reviewers have viewed the evidence base as inconsistent, with scientific testing lacking (Milner et al., 2011), and to a degree this is true. Nevertheless, the current review provides sufficient evidence to implicate river flow as an appropriate variable for ecologically-based river management and restoration, though this approach has rarely been used in practice. Traditionally, river flow management has been the realm of hydrologists and river engineers principally concerned with reducing flood risk while improving, or at least maintaining,

water supply infrastructure (Shaw, 1988; Newson 1994). However there has been growing recognition of the importance of setting environmental flows, with over 250 different procedures now employed in at least 20 countries (Dunbar et al., 2012).

How are environmental flows established?

The reviews of Acreman and Dunbar (2004) and Dunbar et al. (2012) summarised the different methods for establishing environmental flows into four main categories; look-up tables, desktop analysis, functional analysis, and hydraulic-habitat modelling (**Table 3**). These approaches encompass a wide range of scales and situations (**Table 3**), and both reviews concluded that these approaches should not be viewed in isolation, but should form part of a framework (and continuum of methods) where the application of a methodology is determined by factors such as cost, time, perceived environmental risk, availability of expertise, and scale of assessment (whole system through to single site or species). There is a tendency in setting environmental flows to select some aspect of the natural flow regime, for example mean flow or low flow, as a reference point (Richter et al., 1997, 1998, 2003; Poff et al., 2010). However, little reference has been made to the ecological conditions associated with natural flows, possibly due to the confounding effects of other environmental pressures (Bunn and Arthington, 2002; Dunbar et al., 2012), and because few river systems worldwide are unaffected by human activity in some way (Richter et al., 1997; Lytle and Poff, 2004; Welcomme, 2008), which limits the opportunity for identifying the relationship between natural flow conditions and river ecology. Reference condition models, particularly the River Invertebrate Prediction and Classification System (RIVPACS) for macroinvertebrates, go some way to helping establish a reference community (Wright et al., 1998). However, the

adequacy of such models within environmental flow setting is questionable where measured at-site variables (river depth, wetted width and substrate composition) are used for biological prediction, as these variables are likely to naturally vary in response to flow (Harrison et al., 2004). Where alternative variables can be used adequately, this may offer some opportunity to develop similar predictive models for fish communities. In the case of salmonids, and perhaps other river ecosystem components, returning to the natural flow regime may be not always be beneficial, especially in rivers where releases from reservoirs have altered flow significantly and populations appear to be benefitting (Milner et al., 2011). Thus, unnatural flow conditions can be envisaged, such as enhanced summer flows, that might significantly enhance survival and growth at critical periods that might otherwise limit population size or productivity (Nislow and Armstrong, 2012). A further consideration is the impact of a salmonid population that has been 'enhanced' through flow management on ecosystem function. Impacts are potentially detrimental, for example through elevated rates of predation, or might be relatively benign. In the case of lowland rivers in the UK, the majority of which have been highly modified (Brookes, 1988), the concept of what 'natural' means in the context of river flow regime is equivocal. Elsewhere, natural flow regimes may be less ambiguous (Pettit et al., 2001; Lytle and Poff, 2004; Propst and Gido, 2004). In situations where natural flow regime may be difficult to define, flow management might be targeted specifically at generating a temporal pattern of flow to create the conditions that maximize salmonid production. The challenge in this case is to identify what those flow conditions are.

HABITAT MANAGEMENT AND RESTORATION

It is widely acknowledged that a range of pressures affect riverine ecosystems, but there is also a view that given these pressures, it is habitat quality that limits ecosystem function (Ward et al., 2001; Giller, 2005). This view has led to efforts aimed at restoring or rehabilitating river habitat, and as a practice has gained in popularity in river and catchment management over recent decades (Holmes, 1998; Ormerod, 2003; Palmer et al., 2005). The underlying principles employed takes account of the interaction between habitat and river flow by focusing on establishing site or reach scale in-channel features to create hydraulic complexity as guided by geomorphological processes (Kemp et al., 2000; Pretty et al., 2003; Harrison et al., 2004; Newson and Large, 2006; see Roni et al., 2008 for comprehensive review).

A common in-channel approach to targeting salmonid populations is to focus on the availability and quality of spawning gravels to ensure recruitment conditions are optimal. Spawning habitat rehabilitation is a widely used tool in European rivers (Brown and Pasternack, 2009; Pederson et al., 2009; Vehanen et al., 2010). In North America, while the introduction of gravel in sediment-starved river systems has proven beneficial (Merz et al., 2004, 2005), the practice is not common (Roni et al., 2008). Whilst a focus on ensuring successful reproduction makes sense, efforts in this direction appear to have met with mixed or, in some cases, limited success. Pulg et al. (2013) examined the provision of gravel and its regular cleaning as a mechanism for restoring brown trout populations in regulated rivers. The positive effects appeared to be short-lived, which suggests that the maintenance of an appropriate flow regime to replenish spawning gravels and keep them free of fine sediment is a more sustainable approach. Salmonid spawning habitat is highly dependent upon the delivery of suitable spawning

material from upstream to downstream reaches, and the use of hydraulic models may help determine the discharge required to renew the spawning substrate (Hauer et al., 2011). On balance, simply implementing a minimum flow regime alone as part of attempts at management or restoration is unlikely to rehabilitate salmonid spawning habitat, since the geomorphological processes needed to generate the desired physical habitat could be missing (Brown and Pasternack, 2008). In certain situations specific habitat types may be more critical than flow regime. Sukhodolov et al. (2009) showed that braided channels in alpine streams provide refugia for larval and juvenile fish during floods. However, many alpine rivers have lost their braided structure, so restoration of this habitat feature in this instance may represent the priority.

Other categories of river rehabilitation can address riparian rehabilitation, floodplain connectivity, road improvement, and nutrient enrichment (reviewed by Roni et al., 2008). Understanding the ecological benefits of rehabilitation works is important to guiding on-going river habitat management, and poor monitoring programs can be a handicap (Holmes, 1998; Hendry et al., 2003; Giller, 2005). Pederson et al. (2009) advocated an evaluation of gravel re-introduction for salmonids in Danish streams that acknowledged differences in habitat quality among reaches within a river system. To understand habitat quality in a quantitative manner requires a comprehensive monitoring design (Jähnig et al., 2009). One approach is the use of a Before/After, Control/Impact (BACI) design, but even this approach is not without limitations. For instance, it is a common feature of natural systems for populations at two sites to diverge or converge through time, even without an effect resulting from activities at the 'impact' site (Underwood, 1991). Vehanen et al. (2010) used the BACI approach three years prior and post restoration with an unmodified control. Streambed complexity

increased, but no effects on brown trout stocks in rehabilitated areas were detected. Moreover 2+ and older age classes decreased in abundance. A severe drought after the scheme reduced densities of trout to a low level in all streams, overriding any beneficial local effects of rehabilitation. This finding suggests that large-scale regional factors may overwhelm local management efforts, and although suitable habitat exists, flow stress can severely limit restoration efforts.

River restoration is essentially based on a premise that if habitat conditions are suitable, the biota will respond positively, an approach termed the 'Field of Dreams hypothesis'; “if you build it, they will come.” (Palmer et al., 1997). Despite its obvious weaknesses, this approach is often advocated on the basis that a lack of knowledge in quantifying biological processes should not be a barrier to action. A more rational approach, what has been termed 'process-based restoration' (Beechie et al., 2010), is to employ habitat restoration and rehabilitation measures alongside the activities of ecologists that have both field and quantitative skills to design restoration measures, implement monitoring protocols and, what has hitherto been a significant omission, to devise appropriate statistical analyses to demonstrate ecological benefits.

WHAT DATA AND INFORMATION WOULD BENEFIT ENVIRONMENTAL FLOW MANAGEMENT?

A wide range of approaches to environmental flow setting exist worldwide, supported in part by research and expert opinion (Acreman et al., 2005; Roni et al., 2008; Dunbar et al., 2012; Milner et al., 2012). In the UK, attempts have been made to set environmental standards to meet the EU WFD by defining water abstraction limits to protect river systems and appropriate flow releases from reservoirs. These were

established using a combination of site-specific data, expert opinion and stakeholder groups (Acreman and Ferguson, 2010). Many empirical studies worldwide have been conducted at a site-specific level, which provides useful detailed information but for only one or a few sites, so their transferability to unknown sites, or to a catchment scale is questionable (Petts, 2009; Acreman and Ferguson, 2010). Nevertheless widely applicable and generalised models are emerging. For example, Booker and Acreman (2007) analysed data from 63 PHABSIM studies and found strong relationships between single measures of channel form and river hydraulics and the availability of habitat for target species. Estimates of physical habitat sensitivity to flow change from single measures were comparable with full PHABSIM predictions, albeit with greater uncertainty, though some ambiguity may be acceptable in a more risk-based flow setting framework. The modelling approach by Dunbar et al. (2010a,b) has also shown a generic biological response to flow change. A macroinvertebrate community index responded positively to low and high flow and interacted significantly with river channel modification whereby less modified sites had overall higher biotic index scores and appeared to be more resilient to flow reduction. This finding has implications for flow management and restoration by indicating the likely direction of ecological change in response to flow and habitat alteration. The value of this approach is that it can be applied to a range of sites where little or no biological data exist. Notably the models of Dunbar et al. (2010a,b) utilised existing river flow, river habitat and macroinvertebrate data, obtained from a well-established monitoring network of the Environment Agency. This approach tallies with the view of Petts (2009) who proposed that models that incorporate long-term data sets are needed so that population level responses can be predicted.

A potential impediment to translating research results into flow management and restoration measures may be because appropriate expertise is fragmented across the disciplines of ecology, hydrology, geomorphology and civil engineering (Vaughan et al., 2009). An understanding of each field is needed to fully interpret results in order to make sound management decisions; a minimum requirement is that the essential ecological and morphological responses are understood in order to select suitable flow management methods (Jowett, 1997), and move to ecologically sustainable water management (Richter et al., 2003). However, this situation is changing with the recognition of the potential role of hydraulic-habitat modelling (Dunbar et al., 2012).

LONG-TERM DATASETS AND MONITORING

For the management of many ecological systems it is necessary to employ a long-term perspective. Despite the general acceptance of this view, the availability of long-term data to support management remains conspicuously limited (Bayley and Li, 1992; Jackson and Füreder, 2006). Many studies tend to be undertaken over a 3-year time-scale, chiefly a consequence of the typical length of research funding awards, but long time-series data are considerably more valuable and have substantially helped advance our understanding of temporal patterns of abundance (Elliott, 1995; Magurran, 2011). Furthermore, analyses of long-term datasets are more likely to identify spatial and temporal trends that are key to decision-making, something that short-term studies often fail to detect (Poff et al., 2010; Reidy Liermann et al., 2012). Protocols for detecting ecosystem perturbations require comprehensive time-series data for a suite of key indicators (Richter et al., 1996). For example, long-term studies of freshwater macroinvertebrates have improved our understanding of their inter-annual variation and

cycles, biotic and abiotic interactions, and the effects of disturbance and recovery (Jackson and Füreder, 2006). It is important to undertake similar studies of long-lived species, such as salmonids, in order to improve our ecological knowledge, develop suitable models (Elliott, 1995), and detect long-term effects of human impacts on salmonid productivity (Ugedal et al., 2008). In this regard the environmental regulatory bodies are in a unique position to adopt such an approach, and for salmonids they should be able to make best use of existing information from national monitoring programs (Milner et al., 2011), including measures of water quality integrated with management strategies (see Poole et al., 2004 for discussion). Additionally, long-term hydrological datasets are often available for rivers supporting salmonids, and these can provide a detailed history of hydrological change to be considered alongside salmonid and habitat assessment data.

The potential of large datasets has to be considered against the adequacy of monitoring, since current approaches to data collection may be insufficiently specific to permit the confounding effects of autocorrelation between variables to be discerned. This limitation can be overcome to a degree when carrying out hypothesis-led data analyses and model validation, whilst accepting that in some instances monitoring improvements will be needed to ensure they are statistically robust (Milner et al., 2011). However, alterations to monitoring schemes are often viewed unfavourably by organizations that perform these functions; they see it as expensive and potentially render all previous data collection redundant. For salmonids, a parallel approach to the analysis of long-term datasets is needed that uses site-specific studies based upon agreed monitoring protocols so that adequate meta-analyses can be performed (Milner et al., 2011).

CONCLUSIONS

The direct and indirect effects of river flow will affect different fish life-stages in distinct ways but responses appear to be highly variable and attempts to generalise among salmonid species and hydrological regimes has proven problematic. Where river flow has a significant impact on salmonid distribution and abundance, its effects may be imposed over an extended period or over a series of short, but possibly extreme, episodes. Despite these highly variable effects upon salmonid populations, and other river biota, many environmental organizations around the world base their management decisions using relatively simple river discharge values (Acreman et al., 2008). This approach is unsurprising since many have invested significant resources in establishing river flow measurement networks. Additionally, biological monitoring networks have been established, largely in isolation from flow measurement networks, and mainly as a response to industrial pollution and the need to manage water quality. Research to date has shown biological response to flow, but causal links are opaque, possibly due to the correlation between river flow and other environmental variables. Furthermore, other factors that relate to river habitat quality and extent cannot be overlooked. Therefore, although there are developments in continuous simulation models which mean that gauged flows are not always required, the adequacy of the current network of flow and biological monitoring, together with data analysis capability, represent a potential bottleneck to rational management measures and attempts at river restoration for salmonids, and should be reviewed and amended were possible.

Given the current paucity of long-term datasets tailored to salmonid management and restoration, there is a need to consider the value of existing datasets. Analyses applied to large datasets for macrophytes and invertebrates have demonstrated

a range of periodicities in responses to river flow (Dunbar et al., 2010a,b; Acreman and Dunbar, 2011). Furthermore, long-term reductions in flow regime have coincided with reductions in fish populations, though population cycles or trends unrelated to hydrology cannot always be excluded (Bayley and Li, 1992; Acreman and Dunbar, 2011). Empirical models, exploiting long-term data to reveal generalised relationships between flow, habitat quality and macroinvertebrate communities, have been developed which could potentially be applied to assessing river discharge regimes and informing future water resources management (Dunbar et al., 2010a,b), at least in UK rivers for which these data are available. For salmonids there is a pressing need to develop generalised models of flow and habitat requirements that are transferable between river systems (Milner et al., 2011) and, perhaps, species. In order to improve our understanding, and further develop such models, there is a requirement for empirical testing; possibly via adaptive management studies with a common design to ensure subsequent meta-analyses are statistically robust.

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TABLES

Table 1. Life-stage specific impact of contrasting flow characteristics of salmonids among seasons (modified from Nislow and Armstrong, 2012) (NA = not applicable, ? = not known).

	Fry		Parr		Smolt	
Season	Low flow	High flow	Low flow	High flow	Low flow	High flow
Spring	Lower or higher survival	Lower survival	Reduced growth	?	Migratory delay and lower survival	Positive or negative depending on timing
Summer	Reduced growth	Reduced growth	Reduced growth	Increased shelter seeking	NA	NA
Autumn	NA	NA	Reduced growth	?	NA	NA
Winter	NA	NA	Positive or negligible effect on growth	Increased shelter seeking	NA	NA

Table 2. Effects of fine sediment on survival of embryonic stage of salmonids.

Sediment size/description	Effect	Reference
<0.063mm – 0.5mm Silts/clays – coarse sand	Reduced survival in egg stage	Julien and Bergeron (2006)
<0.125mm Silt and fine sand	>0.2% in redds leads to <50% embryo survival	Levasseur et al. (2006)
Clay sediment	Thin film on egg surface reduces oxygen exchange across membrane	Greig et al. (2005)
Fine sediment	>15% fine material in redds deleterious to survival	O'Connor and Andrew (1998)
0.43-0.85 mm	Reduced embryo survival with increased fine sediment. Emergent fry weight also reduced.	Argent and Flebbe (1999)

Table 3. Summary of environmental flow setting categories, example methods, scale of application, and type of situation employed. Adapted from Acreman and Dunbar (2004).

Method category	Example [Country]	Scale of application	Situation type
Look up table	Tennant (Montana) method [USA]	Catchment	Scoping/planning
	Texas method [USA]		
	Basque method [Spain]		
Desktop analysis	Range of Variability Approach (RVA) [USA and others]	Catchment/multiple or single sites	Planning/high level impact assessment
	Resource Assessment and Management framework (RAM) [England and Wales]		
Functional analysis	Building Block Method (BBM) [South Africa and others]	Multiple or single sites	Impact assessment
	Expert Panel Assessment Method (EPAM) [Australia]		
Hydraulic-habitat modelling	Instream Flow Incremental Method (IFIM)/ Physical Habitat Simulation (PHABSIM) [USA and others]	Multiple or single sites	Impact assessment River restoration (including flow regime)
	Computer Aided Simulation model for Instream flow Requirements (CASIMIR) [Germany]		
	River Simulation System (RSS) [Norway]		
	Numerical habitat modelling (NHM) [Canada]		

FIGURES

Figure 1. Identical process controls, but contrasting conditions, leading to either flood flow or low flow in rivers. Modified from Briggs et al. (1997).

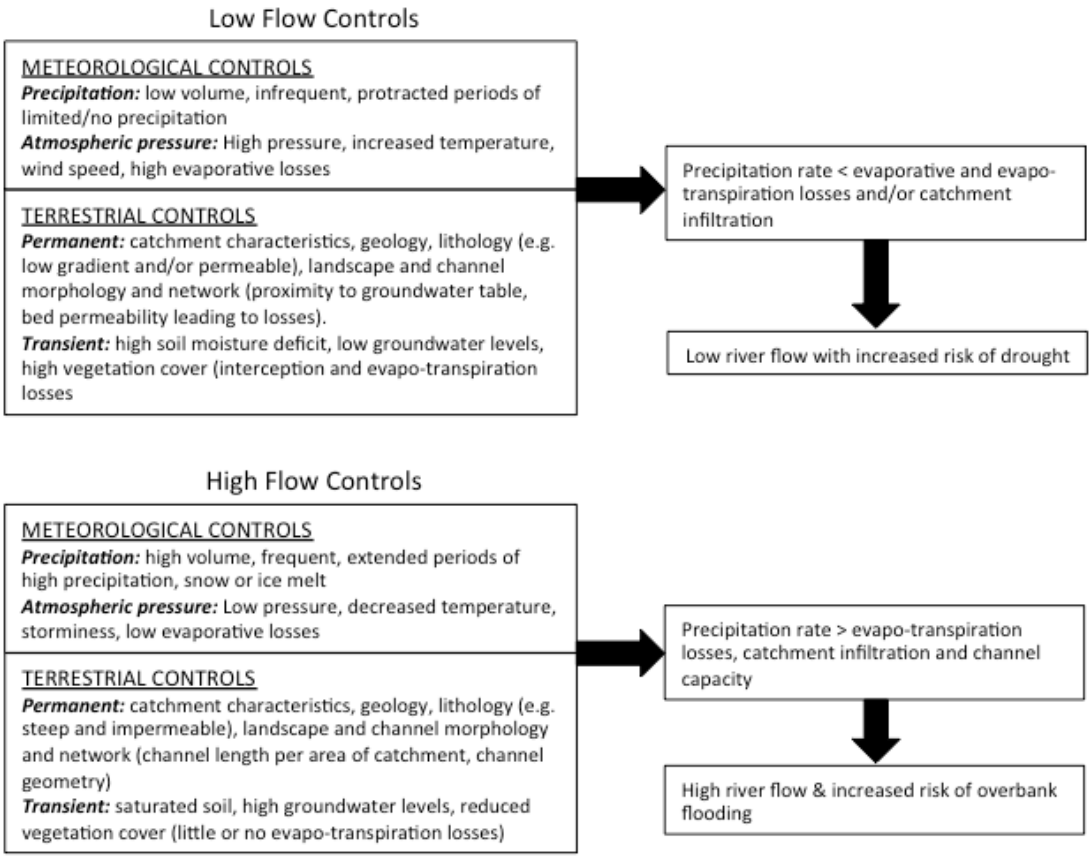
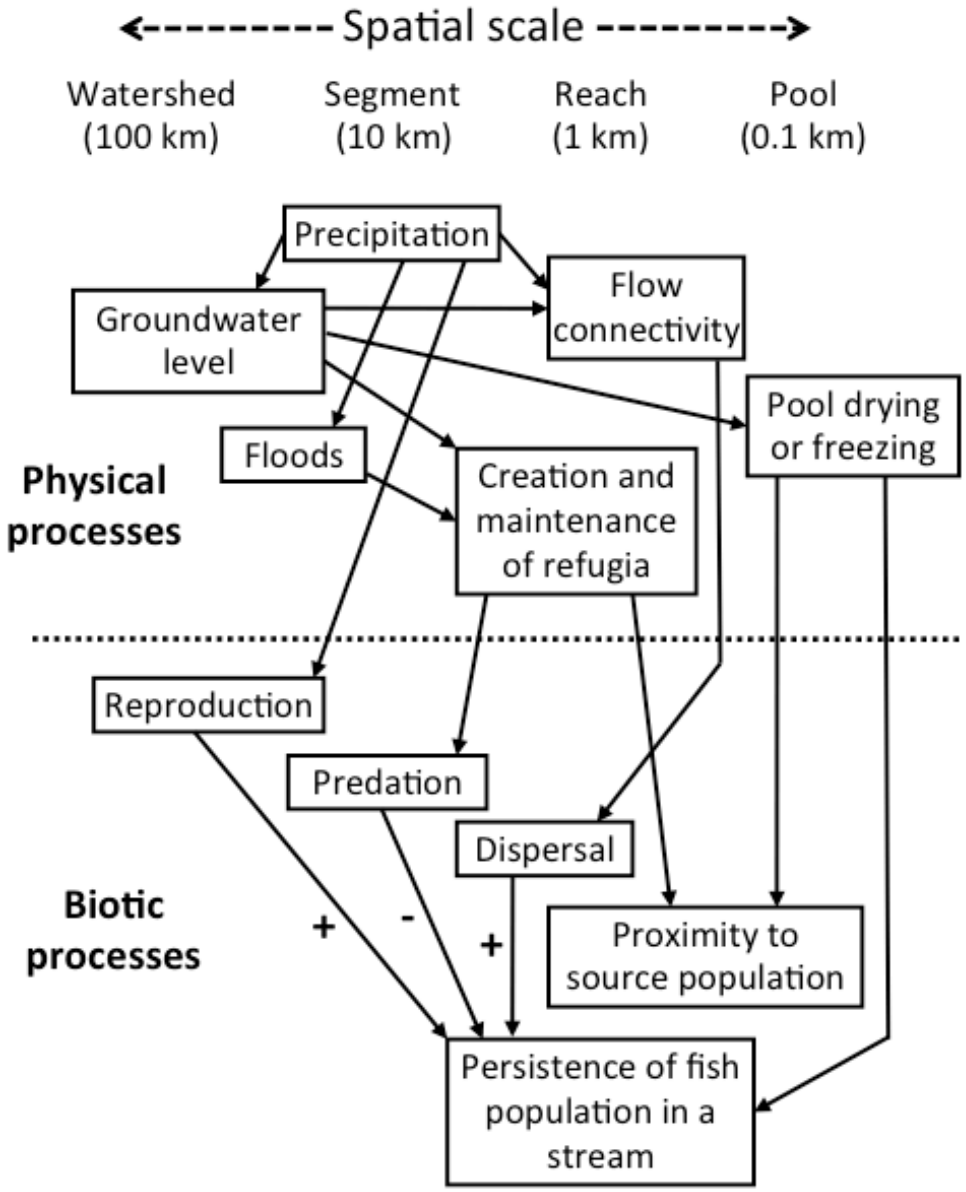


Figure 2. Conceptual model of physical and biotic processes operating at different spatial scales that influence riverine biota within controls imposed by underlying geology/lithology and geomorphology. Modified from Labbe and Fausch (2000).



Chapter Two

BAYESIAN STATISTICS IN ECOLOGICAL MANAGEMENT

ABSTRACT

The way statistics are used in biology, and especially ecology, is changing. Bayesian inference offers an alternative philosophy to the currently widespread frequentist paradigm. Bayesian inference is based around the posterior distribution, a product of a prior distribution set by the investigator and the likelihood of the data. Using Bayes' rule the data update prior understanding to a posterior state of knowledge. Throughout this thesis I have use Bayesian inference in approaching my data analyses, and in this chapter I set out some of the strengths and potential weaknesses of Bayesian inference and argue why it has particular utility in ecological management. Because Bayesian inference allows the data to update our prior understanding to thereby inform our posterior state of knowledge, the approach is logically coherent and offers a powerful approach, particularly in tackling complex hierarchical ecological models. Bayesian inference offers a rigorous framework for handling uncertainty and for translating statistical analyses into ecological decision-making.

INTRODUCTION

The way statistics are used in biology, and especially ecology, is changing. We live in an age of 'new statistics' (Hector, 2015). Effect sizes and confidence intervals are now required by many scientific journals and mixed effects models, information criteria and multimodel inference are routinely applied in biology. And a new enlightened Bayesian world of statistical inference is also emerging. Throughout this thesis I have used Bayesian inference in tackling my data analyses, and in this chapter I set out why I have adopted Bayesian inference and why I believe it has particular application in ecological management. I believe Bayesian statistical inference offers the potential for substantial improvement in practical ecological management. The usefulness and efficiency of Bayesian inference derives from its intuitiveness, simplicity and utility.

FUNDAMENTALS OF BAYESIAN INFERENCE

Bayes' theorem (Bayes and Price, 1763) articulates the relationship between a hypothesis and evidence measured in terms of a probability. In broad terms a probability is simply a 'degree of belief' (with an interval of 0 to 1), 'hypothesis' a conclusion or proposed concept, and 'evidence' can range from anecdote to argument to scientifically collected data. The basic idea underlying Bayes' theorem is that a hypothesis is supported by any evidence that is rendered probable by the truth of that hypothesis; i.e. the probability of a hypothesis increases to the extent that evidence is more likely if the hypothesis were true than if it were false (Zenker, 2013). From a philosophical viewpoint, this concept is simple, logically consistent, intellectually satisfying and uncontroversial (Link and Barker, 2010; Zenker, 2013; Kruschke, 2015).

Verbally, Bayes' rule can be summarised as:

$$posterior \propto likelihood \times prior$$

Thus, the posterior distribution is proportional to the evidence (in the form of data and expressed in the likelihood function) in combination with prior knowledge about the unknowns in a system (Kéry and Schaub, 2012).

If $P(\mathrm{H})$ is the prior or unconditional probability of a hypothesis, $P(\mathrm{E})$ is the marginal or *a priori* probability of the evidence, $P(\mathrm{H}|\mathrm{E})$ is the posterior probability of a hypothesis given the evidence, $P(\mathrm{E}|\mathrm{H})$ is the conditional probability of the evidence given the hypothesis, and it is assumed that $0 < \mathrm{P(H)} < 1$ and $0 < \mathrm{P(E)} < 1$, then Bayes' theorem can be stated mathematically as:

$$P(\mathrm{H}|\mathrm{E}) = \frac{P(\mathrm{H})\,P(\mathrm{E}|\mathrm{H})}{P(\mathrm{E})}$$

There are two fundamentals that distinguish a Bayesian approach to data analysis. First, Bayesian inference quantifies prior beliefs about a parameter in the form of a probability distribution. The second element that characterises a Bayesian approach is the recognition of the 'likelihood principle'. For a given statistical model the evidence derived from a sample that is pertinent to the model parameters is contained in the likelihood function, which describes how the probability distribution of the observed data depend on the statistical parameters that govern the selected statistical model. The prior distribution and likelihood function are combined, resulting in the posterior probability distribution. This distribution reflects our understanding of the statistical

parameters of a model and is used to draw inferences about the parameters of interest in the model. These features of Bayesian inference make the approach distinct from a 'classical' frequentist approach (Link and Barker, 2010).

A COMPARISON OF BAYESIAN AND FREQUENTIST INFERENCE

The key difference in Bayesian and frequentist statistics is in the way in which uncertainty is handled (Kéry and Schaub, 2012). In a frequentist setting, model parameters are modelled as fixed but unknown quantities. In this context, uncertainty is expressed as the variability in hypothetical data sets generated by the model parameters. Probability is derived from the frequency of a specific outcome from these hypothetical data sets, hence a 'frequentist' approach (**Table 1**). A result is that, from a frequentist perspective, it is only possible to make probability statements about the data, not the model parameters. To measure the adequacy of a model in explaining the data a frequentist must use tools such as hypothesis testing and P-values, which are based on the repeatability of observing the data given the model (Link and Barker, 2010). This highlights a serious weakness in classical frequentist statistics, which is that a probability cannot be assigned to model parameters, only about the probability of observing certain kinds of data with a given set of parameter values (Kéry and Schaub, 2012). Null hypothesis testing has been widely criticized (Burnham and Anderson, 2014), and null hypotheses are rarely meaningful and frequently comprise absurd statements that the experimenter knows to be false (Korner-Nievergelt et al., 2015).

Bayesian inference permits fundamentally different conclusions to be drawn with respect to probability. In Bayesian inference probability is a direct measure of 'degree of belief' of an event, parameter value, missing value or prediction. Because

probability is a measure of uncertainty, it is possible to make clear probability statements, given the data, about unknown quantities (Kéry and Schaub, 2012). A key advantage of a Bayesian approach is that is provides probability distributions for the quantities of interest, with the result that probability statements about the magnitude of model parameters can be made with confidence (**Table 1**).

The reason that ecological statistics is firmly rooted in frequentist statistics is partially historical and partially technological. The Reverend Thomas Bayes (1702-1761) formulated his theorem before the advent of null hypothesis testing, which was proposed much later by Fisher (1925). However, solving Bayes' rule without a computer is impossible for all except the simplest models. In contrast, a frequentist statistical framework, being based on the probability of the data given a null hypothesis, are readily soluble for even quite complex models, and as a consequence this approach has hitherto dominated ecological data analysis (see McGrayne, 2011 for a full history). However, the rediscovery of simulation techniques to generate posterior distributions, such as Markov Chain Monte Carlo (MCMC) algorithms (Metropolis et al., 1953; Hastings, 1970), and the advent of sufficiently powerful personal computers that can simulate posterior distributions, means that Bayesian techniques are now more generally accessible (Korner-Nievergelt et al., 2015).

ADVANTAGES OF BAYESIAN INFERENCE

There are a number of benefits to using Bayesian inference in preference to a frequentist approach to data analysis. These are because Bayesian inference is:

Simple

Bayes' theorem is logical and conceptually unambiguous and can readily be applied to complex data and models, including cases where no frequentist methods have been developed. It has particularly proven its value with hierarchical models (Link and Barker, 2010).

Exact

Bayesian inference is a mathematically robust method of analysis. It is based on a sound inferential system and that copes well with small sample sizes and data that include missing values (Link and Barker, 2010).

Coherent

Because of its logical consistency, Bayesian inference represents a coherent and qualitatively simple system of reasoning. Parameters are treated as though they are random variables, permitting them to vary within a model through explicit mathematical expression by means of probability distributions (Link and Barker, 2010; Hilbe, 2014).

Intuitive

Bayesian inference provides a formal mechanism for incorporating and updating prior knowledge. This approach is intuitively appealing, since it reflects the scientific method of acquiring, correcting and integrating previous knowledge (Korner-Nievergelt et al., 2015). Bayesian inference specifically offers the opportunity to attach a probability to a hypothesis of interest thereby permitting informed probability statements about the magnitude of parameters of interest (Gurrin et al., 2000).

PRIORS

The prior distribution is an important feature of Bayesian inference and permits the inclusion of existing information into an analysis, something that is difficult to perform, at least formally, in a frequentist framework. Priors, then, can be viewed as assumptions or predictions (Kéry and Schaub, 2012). Selection of an appropriate prior distribution may be based on information from previous published studies, experience, expert opinion, or theoretical models. Thus prior information serves to link models with previous studies (Prato, 2005), and thereby mirrors the scientific process of accumulating information and using it to update understanding of a system.

Priors can potentially be used as a vehicle to examine alternative assumptions about model parameters by repeating calculations with alternative prior distributions. Data may support a prior assumption, but can also undermine it. The extent to which data lends support to a prior is expressed as the difference between the posterior and prior probability of a hypothesis, in mathematical terms expressed as:

$$P(\mathrm{H}|\mathrm{E}) - P(\mathrm{H})$$

An outcome of this approach is that different prior opinions or evidence can be compared and potentially reconciled.

SUBJECTIVITY

While the opportunity to specify prior distributions is often considered as one of the main advantages of Bayesian inference, it has also been regarded as a key weakness. The chief argument against Bayesian statistics is subjectivity associated with using

priors (Lele and Dennis, 2009; Dienes, 2014; Barker, 2015). In practice, the prior is typically selected to reflect a lack of detailed information, even in cases where an investigator has relevant prior knowledge. Thus 'flat', 'improper' or 'uninformative' priors are routinely used in ecology (Zuur et al., 2014; Kéry and Royle, 2016).

It is worth noting that subjectivity also enters in a frequentist framework. From the formulation of hypotheses, to choosing which data to collect, and deciding which results to finally publish, subjectivity potentially enters at many levels in ecological studies, though it is typically ignored (Korner-Nievergelt et al., 2015)

THE VALUE OF BAYESIAN INFERENCE IN ECOLOGICAL MANAGEMENT

Bayesian inference is increasingly prevalent in ecology (McCarthy, 2007) and is primarily used because it enables direct uncertainty of model parameters and model predictions (Wade, 2000). It is central to formal decision analysis (Berger, 1985), used to assess environmental impacts (Reckhow, 1990), and to structure adaptive management programs (Dorazio and Johnson, 2003). A strength of Bayesian inference, and historically the most controversial aspect, is the facility to allow previous experience or knowledge to be incorporated into new research and associated models. Hamer et al. (2016) coupled prior information from earlier research on amphibians to provide wetland managers with tools to directly assess the efficacy of manipulating water levels in amphibian conservation. Bayesian models have allowed managers to assess the risks to fish populations from alternative land management scenarios (Marcot et al., 2001) and improve river flow conditions for fish of conservation interest (Shenton et al., 2014) and to evaluate management alternatives for river management (Johns et al., 2016).

Bayesian models are useful tools for incorporating expert knowledge of an ecosystem and evaluating potential effects of alternative management decisions to support natural resource management decisions (McCann et al., 2006). These models embody a natural cycle of learning that is well suited to ecological management (Wade, 2000). Bayesian inference provides a framework whereby current knowledge can be updated by new information, so that the results (posterior) of one ecological study can be used as the starting point (prior) for the next. Bayesian models are well suited to provide evidence with quantified certainty for risk assessment and adaptive management situations typical of the ecological management role of regulators, such as the Environment Agency, that claim to be 'evidence based'. As reliance on expert opinion in ecology can be inexact (Drescher et al., 2013), so Bayesian models offer rigor by incorporating opinion with data (evidence). Bayesian models may even be the salvation for ecology as a truly scientific endeavour (Ellison, 1996).

CONCLUSIONS

New statistical approaches and philosophies are available to ecologists. Bayesian inference, in contrast to classical frequentist statistics, uses probability to represent uncertainty about the state of knowledge of a system. Ecological management involves uncertainty, risk and updating knowledge in the light of new data. The key contribution data analysis can provide to ecological management is in improving understanding of uncertainty (both current and future), which is typically substantial in ecological systems. Bayesian methods account for what is known and what is not known and offers a rigorous framework for translating statistical analyses into ecological decision-making.

A NOTE ON REPORTING BAYESIAN INFERENCE

Unlike frequentist analyses where model parameter estimates are viewed as fixed, Bayesian parameters are estimated as posterior probability distributions given the model, observed data and priors. The posterior probability represents a degree of belief about the likelihood of parameters and allow direct probability statements to be made about those parameters. The point of highest density in the posterior probability of a parameter is known as the 'posterior mean'. Strictly, the posterior mean is used when reporting parameter estimates or model fitted values and predictions, estimated using Bayesian inference and I use this terminology throughout my results.

Statistical significance is traditionally used in ecological studies in a frequentist framework, where null hypothesis significance testing against a probability value (typically 0.05) prevails. When assessing statistitical importance using Bayesian models I apply a 95% certainty (other levels of certainty could also have been chosen) that zero is not a possible realisation within the 2.5% and 97.5% quartiles of the posterior mean distribution of model parameters and/or model predictions. Whenever this is the case I use the term 'important' to define a 95% certainty of an effect; i.e. the probability of an effect given the data.

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TABLE

Table 1. Contrasting characteristics of Bayesian and frequentist approaches to data analysis (redrawn from Korner-Nievergelt et al., 2015).

	Statistical approach	
Characteristic	Bayesian	Frequentist
Probability	Probability of a parameter	Relative frequency of an event
Uncertainty	Credible interval	Confidence interval
Information	Prior distribution and data	Data
Significance	Probability of meaningful hypotheses	Null hypothesis test

Chapter Three

THE RELATIONSHIP BETWEEN RIVER FLOWS DOWNSTREAM OF IMPOUNDED LAKES AND JUVENILE SALMONIDS IN THE NORTH WEST OF ENGLAND

ABSTRACT

Anthropogenic changes to river flow regimes are a pervasive problem globally and a major threat to aquatic biodiversity. Flow fragmentation, often in response to river damming, is a particularly severe problem that has a disproportionate effect on migratory species, such as salmonid fishes. Generalised linear mixed models (GLMMs) were used to model the response of juvenile (0+ and 1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) abundance to antecedent flows downstream of impounded lakes used for water abstraction. A clear and positive temporal trend was detected in the abundance of 0+ salmon and trout common to all rivers included in the analysis. Whilst accounting for this temporal change, the models also showed that the abundance of 0+ salmon and trout had a common positive response to the magnitude of summer low flows. The abundance of 0+ salmon and trout showed no response to the magnitude of summer high flows. The abundance of 1+ salmon and trout showed no temporal change and no response to antecedent low flows. The implications for managing flows downstream of impounded lakes to protect and enhance juvenile salmonid survival are discussed.

INTRODUCTION

Flow is acknowledged as a significant source of spatial and temporal heterogeneity in lotic systems. Flow drives a number of physical and biological aquatic processes at different spatio-temporal scales (Poff et al., 1997; Freeman et al., 2001; **Chapter 1**). These processes influence the distribution and abundance of biota and flow regimes can thereby, directly or indirectly, determine the spatial and temporal distribution of fish (Jowett et al., 2005; Poff and Zimmerman, 2010; **Chapter 1**). As a consequence, human perturbation of flow, either by directly extracting water, regulating rivers using weirs and dams, or indirectly through patterns of land use, can affect fish populations and communities (Freeman et al., 2001; Cattanéo, 2005; Park et al., 2006; Benejam et al., 2010; **Chapter 1**).

Engineering schemes, particularly the construction of dams and weirs, but also the regulation of rivers for flood defence can have particularly significant effects on flow (Northcote, 1998; Lucas and Baras, 2001). The effect of these schemes is to modify the flow regimes of rivers, and to present obstacles to fish, which often result in rapid declines in the population size of migratory species, such as salmonids (Beechie et al., 2006; Wootton and Smith, 2015). Some dams completely block the river channel, preventing fish from reaching spawning sites. Other dams may permit fish to pass to varying degrees, but so modify the environment, for example by creating reservoirs, that migration success is reduced. Dams can also cause changes to the thermal regime and oxygen conditions of rivers. Water released from dams can be depleted of oxygen, with devastating effects on fish populations downstream. Alternatively water can be supersaturated with oxygen, which is also damaging to some fishes (Northcote, 1998; Lucas and Baras, 2001). Notwithstanding the effects on water temperature and

dissolved oxygen, the primary effect of river impoundments is to fragment the natural flow of a river. There are numerous examples of negative impacts of dams on migratory fish populations. For example, on the Snake River, situated in the River Columbia Basin in the Pacific northwest of the USA, the construction of hydropower dams has lead to the virtual extinction of migratory Chinook salmon (Kareiva et al., 2000).

In this chapter the effect of changes to flow due to impoundment on salmonid fishes was investigated in four rivers in the north west of England. The lakes are used for public water supply by the water company United Utilities and the flow regimes of the study rivers are largely dictated by water abstraction from the lakes. There are various abstraction licence conditions that ensure downstream river flows are maintained for other water users, with the goal of avoiding the drying of rivers. However, the licence conditions have no specific ecological target, and so are not considered 'environmental flows' and no ecologically-based flow targets are currently in place. Droughts in the mid-1990s led to the use of drought orders and permits by the water company in order to ensure security of water supply to the public. This increase in abstraction resulted in historically low flows in the downstream rivers and raised concerns over the risk to salmonid populations from future drought orders and permit use. As a result, increased fish monitoring was implemented by United Utilities and the Environment Agency (EA) to gain a better understanding of the response of juvenile salmonids populations to flow variability alteration.

All fish survey sites were located in the mid to upper reaches of the study rivers where spawning and nursery grounds occur and provide the preferred habitat for juvenile salmonids. Flows in these reaches were likely to be most affected by river flow alteration from lake abstraction management as flows would not have accumulated due

to the low number of small tributary streams in these reaches. The fish survey reaches were worst affected hydrologically and, potentially, ecologically due to their importance for juvenile salmonids.

The aim of this study was to model the response of juvenile (0+ and 1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) abundance to antecedent flows downstream of impounded lakes, while accounting for temporal trends in abundance.

METHODS

Study sites

The four study rivers discharge from impounded lakes located in the Lake District National Park, Cumbria, England (**Figure 1**). The River Cocker (**Figure 2**) flows north out of Crummock Water for 13 km to a confluence with the River Derwent in the town of Cockermouth. The Derwent flows west for 16 km before entering the southern end of the Solway Firth and the Irish Sea. The River Eamont flows north easterly from Ullswater (**Figure 3**) and passes Penrith after 8 km before joining the River Eden after a further 9 km. The Eden flows north westerly to Carlisle then west to Bowness on the Solway estuary where it meets the Rivers Esk and Annan before entering the Solway Firth. The River Ehen (**Figure 4**) flows west from Ennerdale Water for 4 km then south west for 8 km to pass through the town of Egremont. This river flows in a southerly direction close to the coast for 8 km before joining the River Calder and enters the Irish Sea at Sellafield. The River Leven (**Figure 5**) flows south west from Lake Windermere for 10 km entering Morcambe Bay at Greenodd Sands.

Data analysis

Fish survey data

Counts of juvenile Atlantic salmon (hereafter 'salmon') and brown trout (hereafter 'trout') were obtained from the EA National Fish Population Database (NFPD), which is the repository for all routine electric fishing surveys. The survey data for the study rivers cover the years 1999 to 2010 at 35 sites across the four rivers (**Figures 1 - 7**). In addition to the raw counts of fish, the survey data also included information on the area of river netted off for electric fishing (survey area). Fish surveys were a mix of single pass, double pass and triple-pass electric fishing 'runs'. Here only the first pass of multiple pass surveys were used and incorporated with single pass survey data to standardise data collected among surveys.

River flow data

Data from a river flow gauge on each river encompassing the survey period were obtained, and two time-varying summary flow statistics, Q_{95} and Q_5, were calculated from the gauged daily mean flows. The Q_{95} flow statistics represent antecedent summer low flow (the flow rate exceeded 95% of the time). The Q_5 is the summer high flow (flow rate exceeded 5% of the time). Flow data were obtained for the 121-day period from April 1 to July 31 in each year. This period was chosen *a priori* to represent the flow regime conditions experienced by 0+ salmonids after emergence from spawning redds in late winter/early spring through to the late summer/autumn fish survey season. This period also encompasses the period that 1+ salmonids experience over-summer flow conditions.

Statistical analysis

Before fitting statistical models, a data exploration was undertaken following the protocol in Zuur et al. (2010). The data were examined for outliers in both response and explanatory variables, homogeneity and zero inflation in the response variables, collinearity between explanatory variables, and the nature of the relationships between response variables and explanatory variables. Seven influential outliers for survey area were found in the dataset and removed, resulting in 299 observations for analysis. Removal of outliers led to a reduction of 2.2% in the number of observations and was considered acceptable.

Generalised linear mixed models

Poisson GLMMs were initially fitted to the data with the counts of 0+ and 1+ trout and salmon as the response variables and a log-link function between the response predictor function containing the explanatory variables. Models were structured as:

$$Count_{ijk} \sim Poisson(\mu_{ijk})$$

$$E[Count_{ijk}] = \mu_{ijk}$$

$$\text{var}(Count_{ijk}) = \mu_{ijk}$$

$$\log(\mu_{ijk}) = \eta_{ijk}$$

$Count_{ijk}$ = the kth count of fish from species j, at site i

where site (i) = 1…35

species (j) = 1…2

count (k) = 1…299

$$\eta_{ijk} = \beta_1 + \beta_2 \text{ x } Species_j + \beta_3 \text{ x } Year.std_{ijk} + \beta_4 \text{ x } SumQ95z_{ijk} + \beta_5 \text{ x } SumQ5z_{ijk} + \beta_6 \text{ x } Surv.std_{ijk} + \beta_7 \text{ x } Species_j \text{ x } Year.std_{ijk} + \beta_8 \text{ x } Species_j \text{ x } SumQ95z_{ijk} + \beta_9 \text{ x } Species_j \text{ x } SumQ5z_{ijk} + \beta_{10} \text{ x } Species_j \text{ x } Surv.std_{ijk}$$

$$a_i = N(0, \sigma^2)$$

where η_{ijk} contains 10 parameters consisting of main terms (Species, Year.std, SumQ95z, SumQ5z, Surv.std) and interaction terms (Species x Year.std, Species x SumQ95z, Species x SumQ5z, Species x Surv.std).

Species = 2 level factor (Salmon or Trout)

Year.std = standardised Year

SumQ95z = standardised summer low flow

SumQ5z = standardised summer high flow

Surv.std = standardised fish survey area

Models were fitted to the following response variables:

1. Abundance of autumn 0+ salmonids (trout and salmon)
2. Abundance of autumn 1+ salmonids (trout and salmon)

Model parameters were estimated in a Bayesian framework (**Chapter 2**) using JAGS (Plummer, 2003) and the *R2jags* package (Su and Yajima, 2012) in the R statistical environment (R Development Core Team, 2016). Continuous covariates for parameter estimation were standardised to aid mixing in the Markov Chain Monte Carlo (MCMC)

process. Three independent Markov chains were run simultaneously for each parameter with a burn-in of 5,000, thinning rate of 10 and 40,000 iterations, which resulted in 12,000 Markov Chain samples for each estimated parameter. Mixing (stationarity) and autocorrelation of chains were checked visually using trace plots and the Gelman-Rubin statistic (Brooks and Gelman, 1998). Autocorrelation was low and convergence was achieved in each case.

Each model underwent validation to assess if assumptions for such a model were met. Critically, for models where the response variable was a count, the primary check was whether assumptions for dispersion were met. To check this the models were also used to simulate data using the Poisson distribution within the JAGS model-fitting process. This procedure allowed the fitted values for models using the actual survey data to be compared with the fitted values for the simulated Poisson distributed data. Probability values were used for each data point to assess dispersion. Probability values of close to 0.5 indicate that the Poisson distribution is suitable and over-dispersion is absent. Values close to 0 or 1 indicate over-dispersion associated with an inappropriate distribution used in the model or other model mis-specification (Zuur et al., 2013). Probability values for the 0+ and 1+ salmonid Poisson models were close to 0 and 1 so did not support the use of Poisson GLMMs.

Negative Binomial GLMMs were then fitted to the data with the counts of 0+ and 1+ trout and salmon as the response variable and a log-link function between the response predictor function containing the explanatory variables. Models were structured as:

$Count_{ijk}$ = the kth count of fish from species j, j = 1,..2, at site i

$Count_{ijk} \sim NegBin(\mu_{ijk}, \theta_j)$

$E[Count_{ijk}] = \mu_{ijk}$

$\text{var}(Count_{ijk}) = \mu_{ijk} + (\mu_{ijk}^2 / \theta_j)$

θ_j = dispersion parameter for the variance of the negative binomial distribution and allowed to differ for each species (j) in the models

$\log(\mu_{ijk}) = \eta_{ijk}$

$$\eta_{ijk} = \beta_1 + \beta_2 \text{ x } Species_j + \beta_3 \text{ x } Year.std_{ijk} + \beta_4 \text{ x } SumQ95z_{ijk} + \beta_5 \text{ x } SumQ5z_{ijk} + \beta_6 \text{ x } Surv.std_{ijk} + \beta_7 \text{ x } Species_j \text{ x } Year.std_{ijk} + \beta_8 \text{ x } Species_j \text{ x } SumQ95z_{ijk} + \beta_9 \text{ x } Species_j \text{ x } SumQ5z_{ijk} + \beta_{10} \text{ x } Species_j \text{ x } Surv.std_{ijk}$$

$a_i = N(0, \sigma^2)$

see η_{ijk} for the Poisson GLMMs (described above) for explanation of model terms used.

The negative binomial GLMMs contained the same paramaters, random effects and number of observations as the Poisson GLMMs and were fitted with the same response variables (counts of 0+ and 1+). Initially a single theta (θ) within the negative binomial models was estimated to quantify variance in the count of fish for both species. Initial results suggested that salmon abundance appeared to be greater and also more variable than trout abundance. To account for this subsequent models were fitted that estimated a theta for each species (j) to better reflect the differences in variability. Model parameters were estimated using the same framework as the Poisson GLMMs described above using JAGS the *R2jags* package within the R statistical environment. Three independent Markov chains were run simultaneously for each parameter with a burn-in of 5,000, thinning rate of 10 and 40,000 iterations, which resulted in 12,000

Markov Chain samples for each estimated parameter as per the Poisson GLMM. Mixing (stationarity) and autocorrelation of chains were checked visually using trace plots and the Gelman-Rubin statistic. Autocorrelation was low and convergence was achieved in each case.

To assess dispersion the negative binomial models were also used to simulate data using the same procedure as for the Poisson GLMMs, this time using the negative binomial distribution within the JAGS model-fitting process. Probability values for the 0+ and 1+ salmonid models were 0.65 and 0.54 respectively and support the use of negative binomial GLMMs. Further model validation showed no evidence of heterogeneity, non-linear patterns or spatial correlation in the model residuals (Zuur et al., 2013). Priors placed on model parameters are summarised in **Table 1**.

The goodness of fit for the models was assessed using an 'out of sample' prediction method (see Zuur et al., 2014 & Lunn et al., 2013 for examples and technical explanations). To apply the out of sample technique 10% of the raw data are randomly omitted and the models fitted to the remaining 90% of the data. The posterior mean distribution of the count of salmon and trout are then estimated from the model using the explanatory covariate values from the omitted 10% of data. The estimated posterior mean distribution of counts is then compared with the actual observed counts of salmon and trout to see if the observed value is within the estimated posterior distribution. The closer an observed value is to the centre of the posterior mean distribution of predicted counts suggests that the model has good predictive capability and fits observed data well. The results of the out of sample method are given in **figures 8 and 9**. The 0+ model had 38% of observed counts within the estimated posterior mean distribution while the 1+ model had 72%.

RESULTS

0+ salmonid model

Overall the abundance of 0+ salmon was clearly greater than the abundance of 0+ trout over the study period (**Table 2**), mean site count of salmon was 40.84 compared with 4.95 for trout. There was an important increase in the abundance of salmon through time (**Figure 10**, **Table 2**), the Year.std parameter estimate was strictly positive with no zero in the credible interval, and the posterior mean site count increased from 23.18 to 68.14 between 1999 and 2010. There was also an important increase in the abundance of trout through time, the posterior mean site count increased from 4.18 to 5.96 between 1999 and 2010 (**Figure 10**). Salmon showed an important and positive relationship with summer low flows, and the SumQ95z parameter estimate was strictly positive with no zero in the 95% credible interval (**Table 2**). The posterior mean site count of 0+ salmon increased from 22.10 to 110.46 along the summer low flow range (**Figure 11**). The relationship between summer low flow and 0+ trout, was also important, the posterior mean site count increased from 3.30 to 10.03 along the summer low flow range (**Figure 11**). There were no important relationships between either 0+ salmon or trout and summer high flow or survey area due to the presence of zero in the credible intervals for these parameter estimates (**Table 2**).

1+ salmonid model

No clear temporal change was detected for 1+ salmon or trout, with year parameter estimates containing zero in the 95% credible intervals for both species (**Table 3**). Both species showed no relationship with summer low flow, summer high flow or survey area (**Table 3**). There were clearly more 1+ salmon than trout over the study period (**Table 3**). Overall results suggest that the abundance of 1+ salmonids in these study

rivers have not clearly changed over the study period and showed no relationship with summer flows or survey effort.

DISCUSSION

The primary aim of this study was to model the abundance of juvenile brown trout and Atlantic salmon in relation to antecedent summer flows downstream of impounded lakes used for public water supply. Flow in the rivers was strongly dependent on lake water abstraction management. Results suggested that while accounting for temporal trends, summer (April to July) low flows had an important positive influence on late summer and early autumn abundance of 0+ salmonids and could benefit first summer survival (Nislow and Armstrong, 2012). This effect could be related to stable summer low flows that were maintained artificially higher than natural by the releases of water from the managed lakes (Gustard et al., 1987). As such, juvenile salmonids may not experience the lowest flows that could occur naturally in dry summers, with associated negative effects on survival and growth (Nislow et al., 2004; Davidson et al., 2010; **Chapter 1**). Thus, the maintenance of stable summer low flows from lake releases may have enhanced 0+ salmonid survival.

Despite the clear temporal trend and positive relationship with summer low flow, there was no relationship detected between the abundance of 0+ salmonids and summer high flow. Again this finding could have been because the lowest summer flows were more important for the post-emergence stage that is considered to be a critical life stage for juvenile salmonids (Elliott, 1995; Milner et al., 2003). These flows were more likely to control the amount of aquatic habitat available to newly emerged fish under strong

density-dependent regulation. Reduction in habitat due to extreme low flows can increase local densities leading to high mortality, so the maintenance of stable low flow conditions from managed lake releases could be the overriding implication for river flow conditions for 0+ salmonids in these rivers.

The lack of important relationships between 1+ salmonids and either of the summer flow variables might also be explained by the greater importance placed on summer low flows enhancing the survival of 0+ fish and subsequent smolt production (Hvidsten et al., 2014). Furthermore, the ability of 1+ salmonids to move between habitats within a reach in response to changing flow conditions is an adaptive behaviour that enhances growth and survival (Gross, 1987; Jonsson and Jonsson, 2011). A result is that 1+ salmonids are not as directly dependent on flow conditions as the 0+ age class, resulting in more subtle relationships with low flow (Nislow and Armstrong, 2012) which exhibit strong site fidelity. An assumption is that habitat quality and availability are adequate to maximize the fitness of individuals actively migrating between habitats and may highlight the importance of the interaction of physical habitat quality and river flow (Milner et al., 2003). Information on habitat quality for this study was unavailable, but if available could have been incorporated into the model to explore such interactions.

There were clearly more juvenile salmon than brown trout and this outcome is noteworthy. The cause of the observed interspecific differences in abundance is unclear and a suite of explanations are credible. There is good evidence that emergence times and early stage habitat needs overlap between salmon and trout, with potential for competition dependent on the spatial arrangement of preferred habitats (Heggenes et al., 1990; Armstrong et al. 2003). Trout are considered more aggressive than salmon and can restrict the habitat use of salmon, but their relative distribution within streams is

thought to be determined by flow and habitat type (Heggenes et al., 1990). Juvenile salmon are associated with faster flowing water and shallow habitats compared with juvenile trout which prefer slower flowing water close to bankside cover (Armstrong et al., 2003).

Interspecific competition is not inevitable and is dependent upon other population processes such as predation and climatic events (droughts or floods) and when these factors regulate populations competition is minimised or non-existent (Hearn, 1987). The long-term coexistence of salmonid species, in these and other rivers, is likely to be facilitated by species differences in habitat and associated differences in aggressiveness, innate habitat preferences, timing of larval emergence, morphology, or a combination of these factors (Hearn, 1987; Skoglund et al., 2011). There is also likely to be some degree of plasticity in behavioural strategies for both of these species (Harwood et al., 2002). Such considerations may need to form part of river flow management and an attempt to more explicitly quantify them in order to combine this information with that for flow in statistical models.

Neither species nor their age classes within species showed any relationships with sampling effort (survey area) suggesting that the numbers of caught fish is invariant to sampling effort leading to a loss of sampling efficiency as survey effort increases. Problems can arise when the catch and survey effort are combined into a Catch Per Unit Effort (CPUE) index, typically in fisheries this is expressed as $N\ m^{-2}$ and often extrapolated to $N\ 100\ m^{-2}$. Extrapolating in this way assumes that either capture probability remains constant (Gwinn et al., 2016) and/or that fish are distributed in a homogenous manner across sampling units (Bayley and Austen, 2002). Neither assumption is likely to be met, with implications for juvenile salmonid monitoring

strategies by fishery scientists and river managers.

The effects of flow regime management have been proposed to be life stage specific (Nislow and Armstrong, 2012). The approach using mixed models adopted in the present study appears to support that view. Further analyses using data from other regions are required to determine the generality of the relationships found here.

Most compensation discharges in the UK have been set to satisfy river interests that no longer exist, and were based on inadequate hydrological or biological information resulting in a wide range of flow release patterns (Gustard et al., 1987). Coordinated adaptive management schemes with river flow trials are needed in order to assess the ecological response to altering current flow release practices. This approach will require robust study design and analyses, ideally within a Bayesian framework (**Chapter 2**), to test expert opinion and incorporate prior belief using results from studies such as this one.

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TABLES

Table 1. Diffuse priors used in models. NA = not applicable. *half-Cauchy(25) distribution = norm (0, 0.0016) / norm (0,1), see Marley and Wand (2010).

Prior	Distribution	Estimation within JAGS
Betas	norm(0, 0.001)	NA
Dispersion (θ) numerator (*θ.num*)	*norm(0, 0.0016)	Dispersion = *θ.num/θ.denom*
Dispersion (*θ*) denominator (*θ.denom*)	*norm(0, 1)	
Random intercept (*ri*) numerator (*ri.num)*	*norm(0, 0.0016)	SD (*ri.sigma*) = *ri.num/ri.denom* Variance (*ri.tau*) = 1/(*ri.sigma*^{2})
Random intercept (*ri*) denominator (*ri.denom)*	*norm(0, 1)	

Table 2. Model parameter estimates (0+ salmonid model). CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold.

Parameter	Posterior mean	Lower CrI	Upper CrI
Intercept (salmon)	3.71	**3.45**	**3.97**
Year.std	0.38	**0.13**	**0.63**
Trout	-2.11	**-2.39**	**-1.83**
SumQ95z	0.38	**0.15**	**0.61**
SumQ5z	-0.04	-0.24	0.16
Surv.std	0.05	-0.13	0.23
Year.std x Trout	-0.25	-0.60	0.10
SumQ95z x Trout	-0.12	-0.45	0.21
SumQ5z x Trout	0.01	-0.29	0.32
Surv.std x Trout	-0.03	-0.28	0.21
Dispersion (θ) Salmon	1.27	**0.98**	**1.62**
Dispersion (θ) Trout	1.22	**0.89**	**1.66**
Random intercept$_{(sigma.ri)}$	0.49	**0.31**	**0.72**

Table 3. Model parameter estimates (1+ salmonid model). Credible intervals that do not contain zero in bold.

Parameter	mean	Lower CrI	Upper CrI
Intercept (salmon)*	1.46	**1.01**	**1.90**
Year.std	0.35	-0.01	0.73
Trout*	-1.44	**-1.89**	**-1.00**
SumQ95z	0.30	-0.05	0.65
SumQ5z	0.15	-0.13	0.46
Surv.std	-0.09	-0.34	0.18
Year.std x Trout	-0.02	-0.57	0.53
SumQ95z	0.21	-0.30	0.73
SumQ5z	-0.36	-0.85	0.12
Surv.std	-0.13	-0.56	0.28
Dispersion (θ) Salmon	0.66	**0.48**	**0.89**
Dispersion (θ) Trout	0.83	**0.46**	**1.46**
Random intercept (*sigma.ri*)	0.97	**0.65**	**1.38**

FIGURES

Figure 1. Location of study rivers and fish survey sites (indicated by red dots). Clockwise from top-left: River Cocker, River Eamont, River Leven, River Ehen.

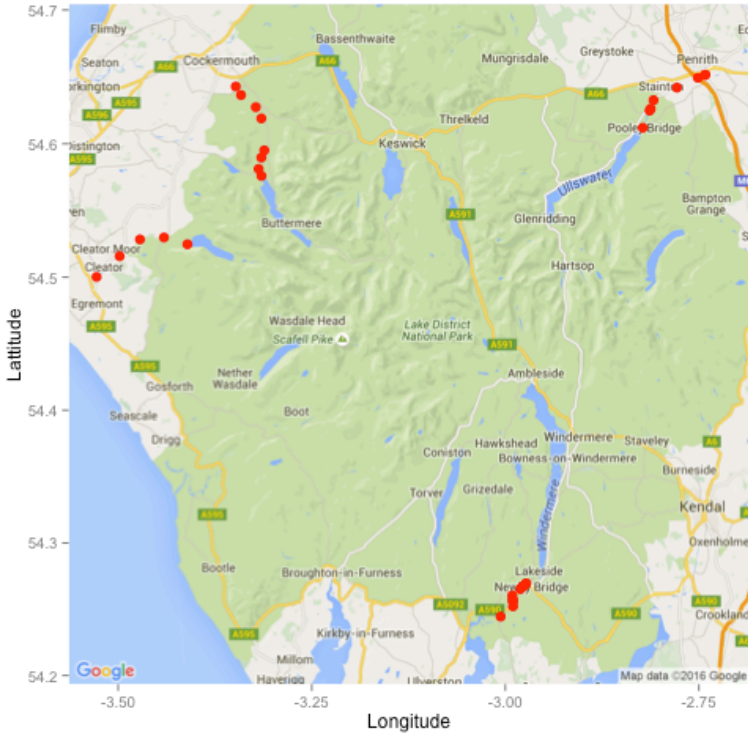


Figure 2. Location of River Cocker fish survey sites (indicated by red dots).

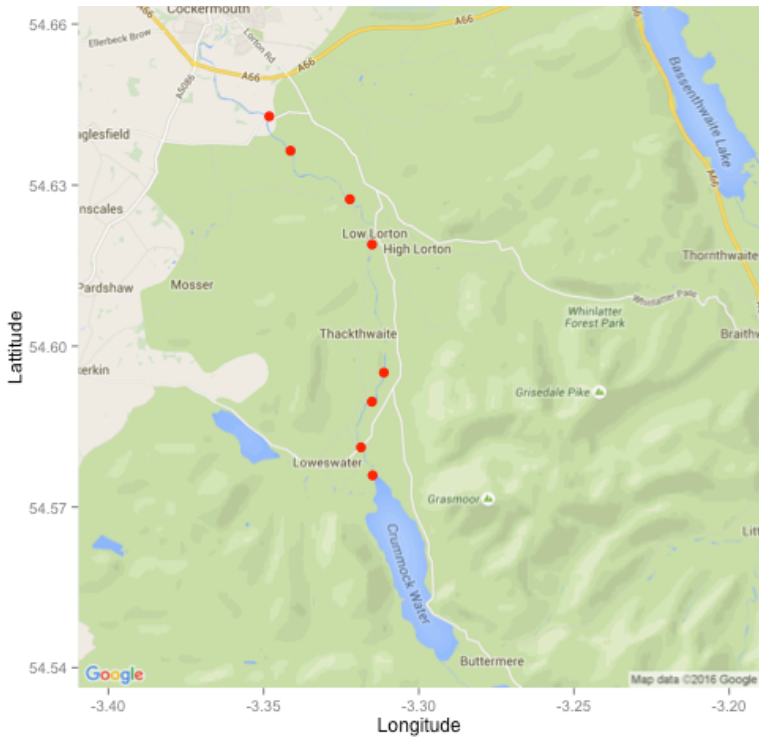


Figure 3. Location of River Eamont fish survey sites (indicated by red dots).

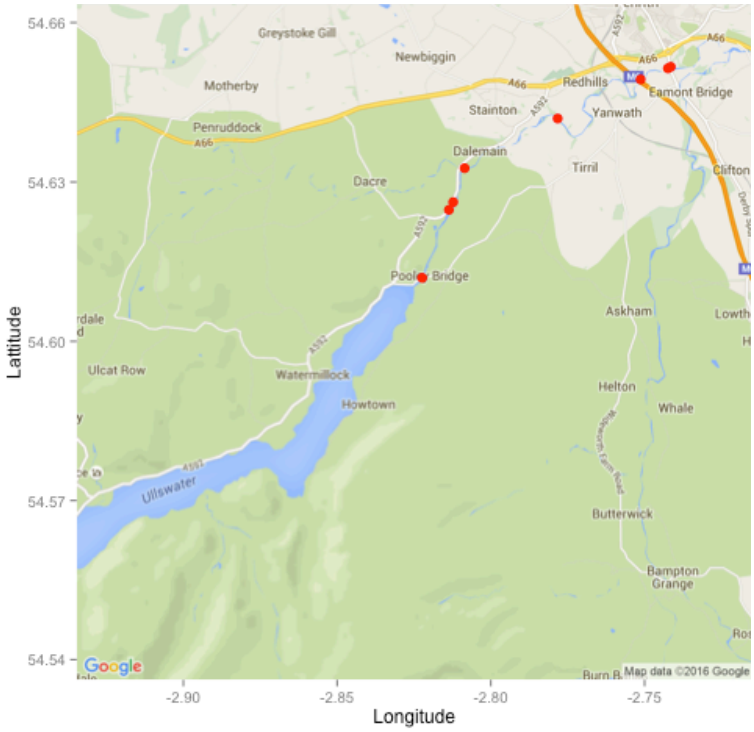


Figure 4. Location of River Ehen fish survey sites (indicated by red dots).

Figure 5. Location of River Leven fish survey sites (indicated by red dots).

Figure 6. Box and whisker plot showing the median and range of counts of 0+ salmonids by species for the study rivers (Cocker, Eamont, Ehen and Leven). SS = Salmon, ST = Trout.

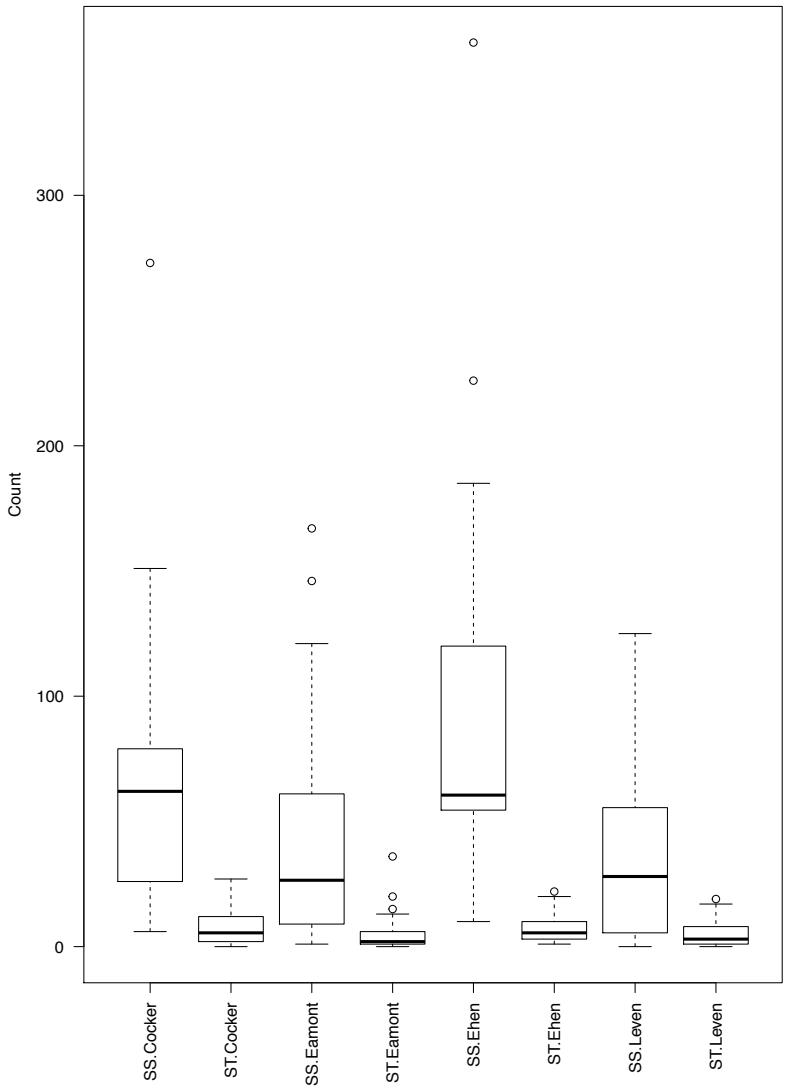


Figure 7. Box and whisker plot showing the median and range of counts of 1+ salmonids by species for the study rivers (Cocker, Eamont, Ehen and Leven). SS = Salmon, ST = Trout.

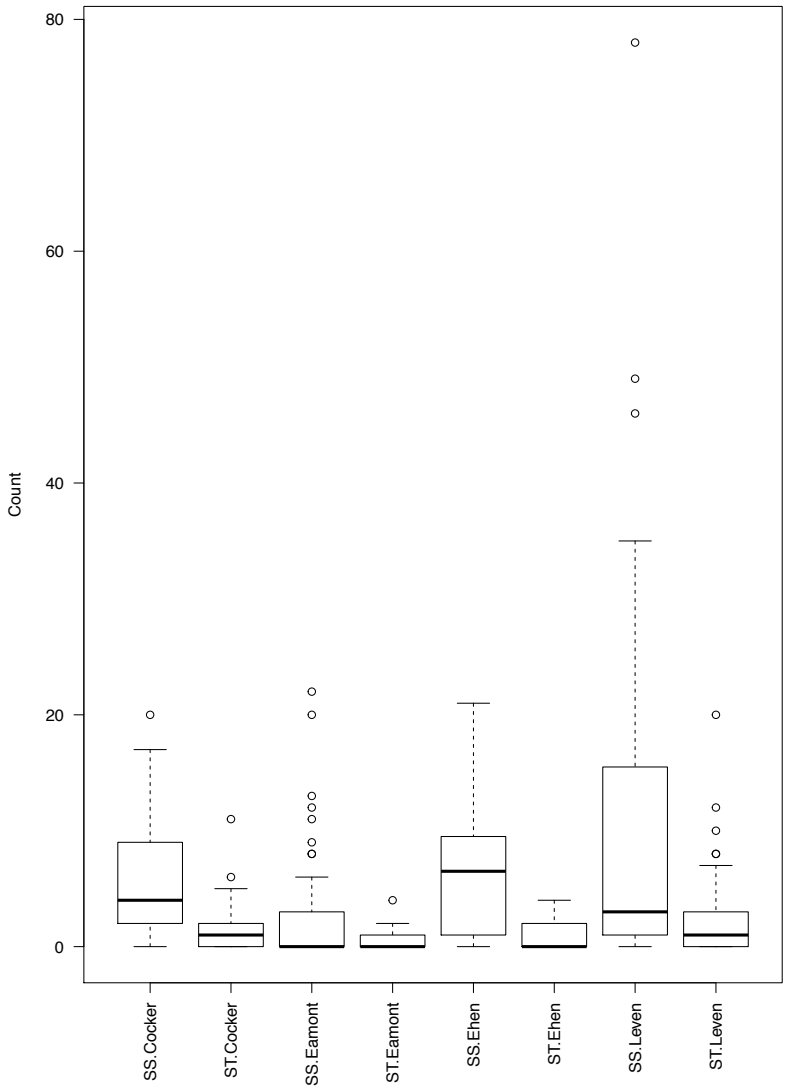


Figure 8. Out of sample prediction results for the 0+ negative binomial model. Each panel represents one omitted count of 0+ salmonids. The posterior mean distribution obtained from the model is shown for each panel. The red dot is the actual omitted count.

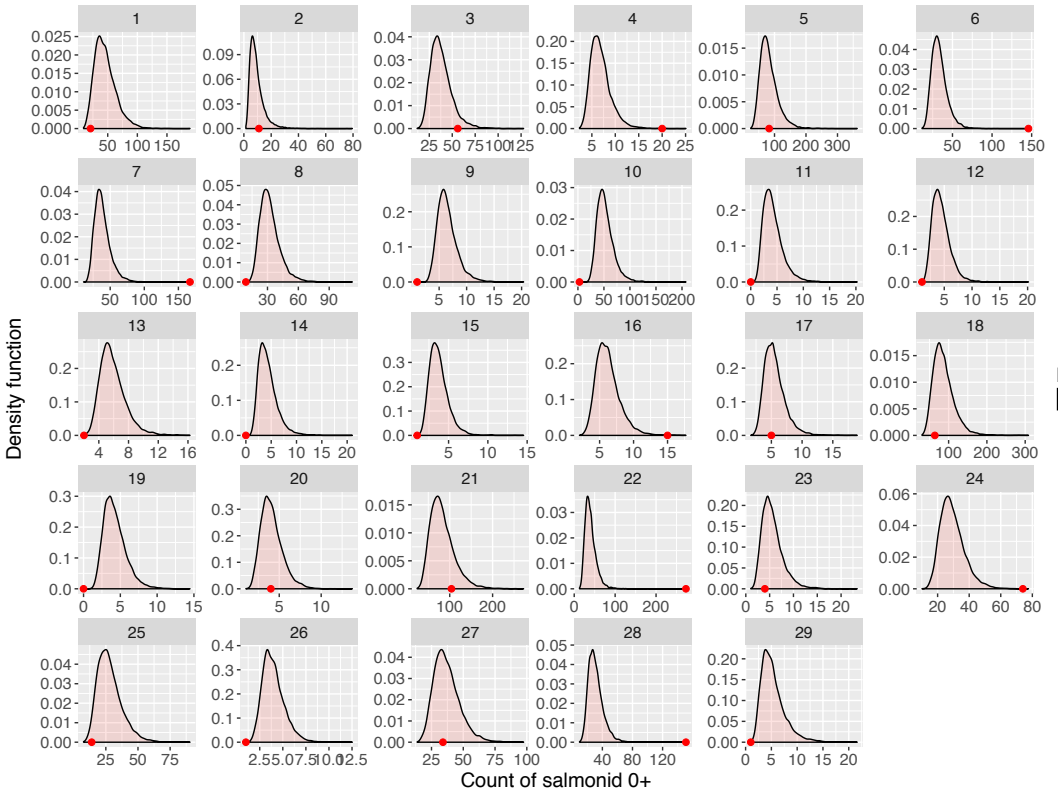


Figure 9. Out of sample prediction results for the 1+ negative binomial model. Each panel represents one omitted count of 1+ salmonids. The posterior mean distribution obtained from the model is shown for each panel. The red dot is the actual omitted count.

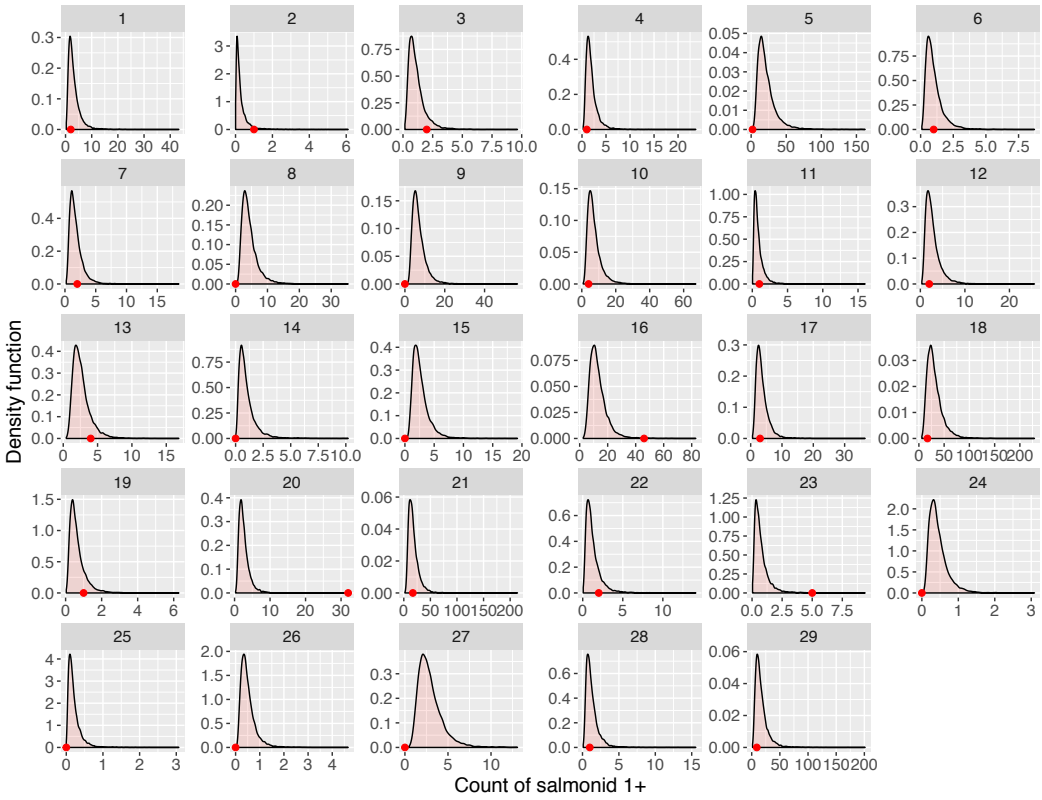


Figure 10. Fitted values for 0+ salmonid abundance among years modelled with a negative binomial GLMM using Bayesian inference. Inner polygon lines indicate posterior mean. Outer polygon lines indicate 95% credible intervals. SS = Salmon, ST = Trout.

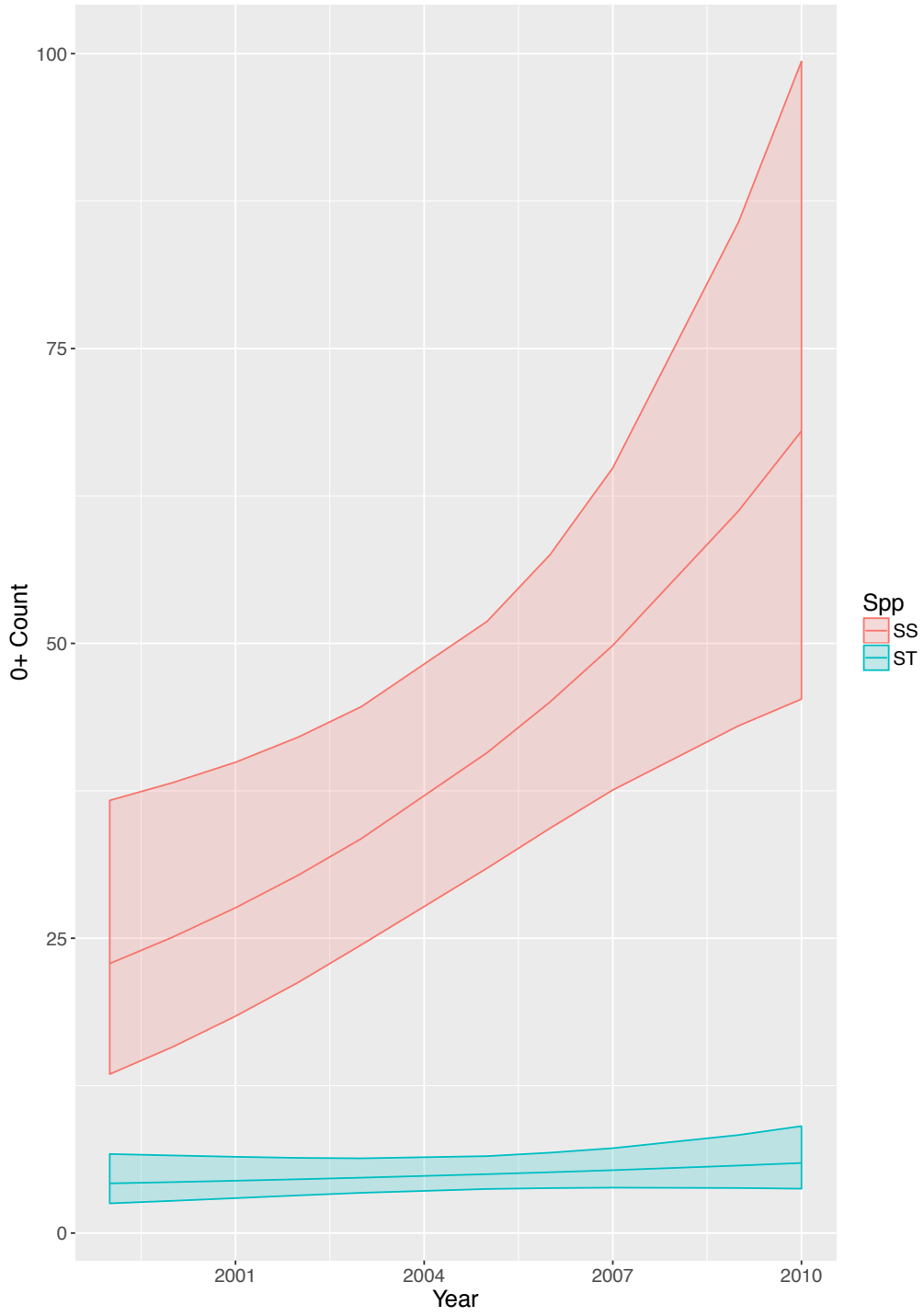
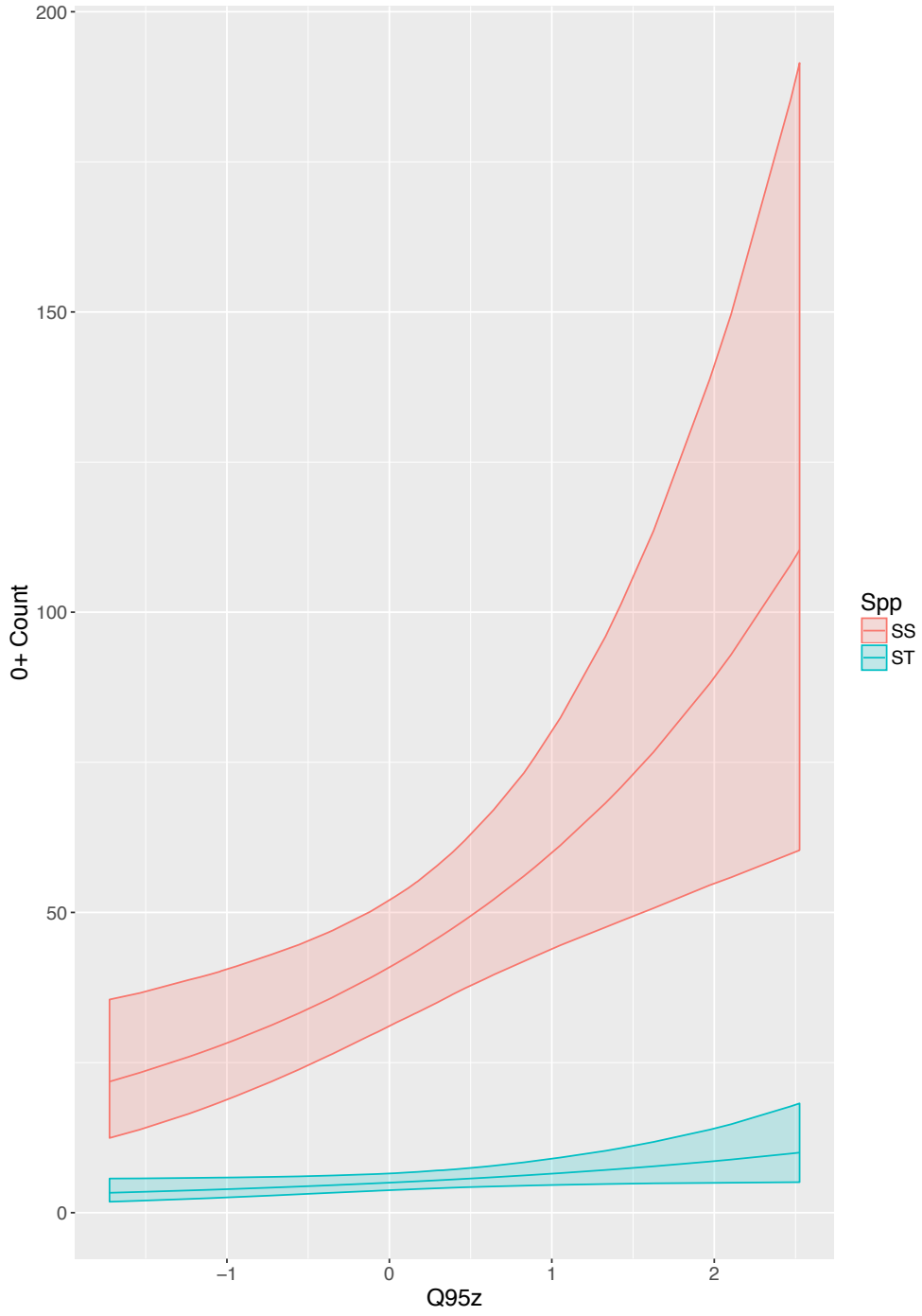


Figure 11. Fitted values for 0+ salmonid abundance as a function of Summer Q95z (summer flow exceeded 95% of the time) modelled with a negative binomial GLMM using Bayesian inference. Inner polygon lines indicate posterior mean. Outer polygon lines indicate 95% credible intervals. SS = Salmon, ST = Trout.



Chapter Four

THE EFFECT OF A SHORT-TERM LOSS OF RIVER FLOW ON A BROWN TROUT POPULATION IN NORTH WEST ENGLAND

ABSTRACT

An important challenge for hydroecology is to better understand and quantify the response of biota to anthropogenic alteration of natural river flows. Rivers below reservoirs tend to have highly altered flow regimes that are dictated by reservoir management decisions governing releases of water. I investigated the effect of a short-term cessation of reservoir compensation flows to the Bradshaw Brook in North West England, UK. Spring and autumn survey data from routine fish monitoring at the impacted river and five other control rivers, were analysed using Generalised linear mixed models (GLMMs) fitted within a Bayesian framework. Models were fitted within a Before-After Control-Impact (BACI) design to test for impacts on 1+ brown trout (*Salmo trutta*) abundance. Subsequent recovery was assessed using Bayesian GLMMs that quantified inter-annual variation across the impacted river and control rivers. Analyses revealed highly important reductions in spring 1+ brown trout abundance at the impacted river during the short period following the flow loss incident in comparison with controls. Analyses using monitoring data from the autumn season, other trout age classes (0+ and 2+), and subsequent years showed that any impacts from the cessation of compensation flows were restricted to spring 1+ trout in 2005 immediately after the loss of flow. This analysis demonstrated that brown trout populations can be directly affected by short-term flow loss, but have the capacity to rapidly recover once flow conditions return to pre-impact levels. Despite recovery in

this instance, this analysis demonstrated that brown trout, and possibly other salmonid species, are potentially sensitive to river flow management practices downstream of reservoirs.

INTRODUCTION

River flow regime is a key variable in maintaining the diversity and functioning of riverine biota (Warren et al., 2015, **Chapter 1**). Alteration of river flows due to water abstraction, impoundments and reservoirs can lead to losses of key flow-dependent processes, such as biological productivity, abundance of organisms, growth rates, and dispersion or migration (Poff et al., 1997; Beechie et al., 2006). The emerging science of hydroecology aims to quantify the links between flow regimes and their anthropogenic alteration with changes in ecological quality (for review see Warren et al., 2015). Although the concept of providing compensation or environmental flows has long been acknowledged, the setting and management of these parameters has rarely had a quantitative ecological basis (Gustard et al., 1987). Reservoir compensation flows in the UK are primarily set to provide a minimum base flow during the summer months, along with 'spate' flows to facilitate upstream and downstream migration of salmonids timed to coincide with specific aspects of their life history. In addition to understanding the magnitude of flow on salmonid life history, the significance of the temporal pattern of flow needs to be understood to permit rational management decisions. Thus, sustained periods of high flow can be extremely damaging to salmonid populations, for instance by washing fish out of the system (e.g. Sato, 2009). Similarly, periods of low or zero flow might have detrimental effects on salmonids, for instance by increasing density-dependent mortality (Elliot et al., 1997). These impacts may have greater

magnitude if they occur at sensitive periods of the life cycle (Warren et al., 2015, **Chapter 1**)

The Environment Agency (EA) identified seven rivers at risk of impact during drought events in their Greater Manchester, Mersey and Cheshire (GMMC) area in North West England (Environment Agency, 2007). These rivers have public water supply reservoirs at their headwaters, which regulate the downstream river flow. A consequence of this situation is a high probability of greatly reduced flows during droughts when demands on reservoir supply are greatest. Extended droughts can result in the implementation of drought orders, which allow short-term flow reductions on rivers to facilitate supply of water to the public. A brown trout drought monitoring programme began in 2000 at five of the seven rivers with the principle aim of measuring the effect of events such as droughts and to use this information in future decision-making for water company drought order applications (Environment Agency, 2007).

During the winter of 2004 the reservoir compensation flow to Bradshaw Brook, one of the rivers at risk and with brown trout monitoring, was accidentally stopped for between six to twelve hours (Environment Agency, 2007). This event resulted in a complete loss of flow in the river downstream of the reservoir and was considered at the time to be a serious environmental incident and led to the prosecution of the water company operating the reservoir and legally responsible for providing flow to the river. As part of the prosecution in 2006 the EA presented a qualitative summary of fish survey data to show that an unusually low number of 1+ trout were subsequently found in the river in the spring of 2005 following the event.

The main aim of this chapter is to reappraise the original EA analysis by fitting Bayesian mixed models to the dataset used in the 2006 prosecution to demonstrate that quantitative estimates, with certainty, can be derived to provide more robust impact assessment evidence. In addition, other age classes of brown trout and survey seasons are considered for the same rivers and time periods. Models are fitted to data from the same rivers but include the most recent years of available survey data, which were not available during the original EA analysis.

To investigate the effects of the flow loss on Bradshaw Brook, brown trout survey data for this river were used along with data from the other rivers in the GMMC area acting as 'controls'. These specifically comprised spring survey data from routine electric fishing surveys. Autumn data were also available, and these were used in subsequent analyses in order to test for effects on autumn trout abundance. These autumn data were supplementary to the original EA investigation in 2006. In addition to analysing autumn abundance data, data for subsequent years, up to and including 2010, were also used in further analyses to measure subsequent recovery of trout abundance. These data were, again, not included in the original EA analysis. Statistical models were fitted to relevant available datasets to address the following:

i. Quantify the impact on spring 1+ trout abundance in 2005 for Bradshaw Brook;
ii. Compare the abundance of spring 1+ trout at Bradshaw Brook in 2005 with the abundance of spring 1+ trout in other years for that river and for other rivers identified at risk from drought and low flows;
iii. Quantify the impact of flow loss on 1+ trout abundance at Bradshaw Brook in autumn 2005;

iv. Quantify impacts on other age classes of trout (0+ and 2+) at Bradshaw Brook in both spring and autumn 2005;

The inference of any ecological response to river flow alteration can be problematic to demonstrate and requires a specific experimental design paired with an appropriate statistical model. The Before-After-Control-Impact (BACI) design is one that is often employed because it controls for confounding temporal and spatial effects (Stewart-Oaten et al., 1986; Underwood, 1992; Smith, 2002). However, a BACI design has limitations, particularly if traditional statistical methods, such as ANOVA and ANCOVA are used that fail to properly accommodate the data structure. In a BACI design, control and impact data are collected on a number of occasions through time; they are repeated measures. These data are likely to show temporal dependency between observations at the same location through time, termed temporal autocorrelation. In addition, 'replicates' within the control and impact locations are likely to exhibit spatial dependency, since they are located in the same ‘treatment’ area, termed spatial autocorrelation. These are non-trivial issues since they directly affect the standard errors, and thus confidence intervals, of estimated model parameters. As a consequence, to assess the impacts of river restoration measures a statistical design is likely to comprise a number of sampling sites or reaches on an impacted river that are mirrored on the control rivers. Such nested data with repeated measures are best analysed with mixed effects models (Pinheiro and Bates, 2000; Zuur et al., 2009).

An additional consideration is the response variable within the chosen statistical technique. Most ecological studies of animals focus on the count of individuals given a rate of sampling; e.g. counts within a survey area to provide an estimate of density.

Applying models that assume a Gaussian distribution for the response variable tends to result in negative fitted values, or realisations around the fitted mean, and assume constant variance around the fitted mean. Count data are bounded by zero and variance tends to increase with the mean, thereby failing the assumptions of Gaussian-based models (O'Hara and Kotze, 2010). Generalised Linear Models (GLMs) are capable of dealing with departures from normality and constant variance by using link functions, exponential family distributions and offsets that accommodate variation in sampling effort (Dobson and Barnett, 2011; Zuur et al., 2009). Generalised linear mixed models (GLMMs) combine the properties of two statistical frameworks; linear mixed models, incorporating random effects and repeated measures, which create inherent spatial and temporal correlation between observations, and generalised linear models outlined above (Bolker et al., 2009; Zuur et al., 2013).

METHODS

Study sites

The study rivers are located in the Environment Agency's Greater Manchester, Mersey and Cheshire (GMMC) area in North West England (**Figure 1**) and all but one, the River Sett, are below reservoirs used for public water supply. Bradshaw Brook flows south out of the Jumbles Reservoir near the town of Bolton in Lancashire (**Figure 2**) and joins the River Croal in Bolton after 7 km before joining the River Irwell, the Manchester Ship Canal then the Mersey Estuary at Widnes. The River Bollin (**Figure 3**) flows from the Teggsnose and Bottoms Reservoirs south east of the town of Macclesfield in Cheshire. The Bollin then flows in a north-westerly direction through Macclesfield, across the Cheshire plain to skirt Manchester then join the Manchester

Ship Canal and the Mersey Estuary. The River Goyt (**Figure 4**) flows north from Fernilee Reservoir in the Goyt Valley on the western of edge of the Peak District National Park. After approximately 8 km the river flows in a north-westerly direction, through the town of Stockport where it joins with the River Tame to become the River Mersey, which then flows into the Manchester Ship Canal. The River Sett (**Figure 5**) flows off the north-western edges of the Kinder Scout moorland massif in the Peak District National Park. It flows for 3.5 km to the village of Hayfield where it then flows westerly to join the River Goyt after approximately 7 km. The River Sett has no reservoir in its upper reaches so does not experience the same flow alteration as the other rivers, it is used by the EA as a 'near natural' flow control so that trout abundances from regulated rivers can be compared with those in the Sett.

All the fish survey sites are in the upper reaches of the rivers close to the reservoirs and are consequently in the zone of maximum influence from reservoir releases. In addition, these reaches support the spawning and nursery areas for brown trout so are considered the most sensitive reaches to flow alteration and dewatering should reservoir flow releases cease.

Study design

Following EA analysis a BACI design was used with Bradshaw Brook as the impacted river and the Rivers Bollin, Goyt and Sett acting as controls. Two other rivers within the EA's area drought monitoring programme were available, these were the River Etherow and Eagley Brook. An initial inspection of available data for these rivers showed gaps in the data in several years for both rivers. The Eagley Brook also had only one brown

trout survey site. Consequently, I chose *a priori* to exclude these rivers from the analyses based on their lack of data and survey site replication.

Fish survey data

Electric fishing surveys were undertaken using fully standardised quantitative procedures that are set out in EA monitoring guidance. Captured fish were measured for Total Length (TL) to the nearest 1 mm and scales were collected from a subsample for age analysis using growth checks. Fish age classes were derived from both scale-ageing assessment in the lab and site-specific length-frequency analysis using standard fisheries procedures.

Spring (May and early June) and autumn (September and October) electric fishing survey data were obtained from the EA National Fish Population Database (NFPD). Available data were extracted for 15 survey sites across the four chosen rivers in the EA's GMMC area for an eleven-year period (2000-2010 inclusive), providing 269 estimates of fish abundance. The full dataset was divided into separate datasets based on the age classes of fish (0+, 1+ and 2+), a summary of the survey results for each class are given in **Tables 1** to **3**.

Data exploration

Before applying statistical models a data exploration was undertaken (Zuur et al., 2010). The data were examined for outliers in the response and explanatory variables, homogeneity and zero inflation in the response variable, collinearity between explanatory variables and the nature of relationships between the response and

explanatory variables, including spatial and temporal autocorrelation. Data exploration was performed using R statistical software (R Development Core Team, 2016).

Statistical modelling

Following data exploration, statistical models were fitted and validated to ensure all model assumptions were met. Since data were collected in consecutive years from 15 sites within 4 rivers a mixed modelling approach was used to accommodate repeated sampling of the same sites among years. Fish surveys recorded trout abundance as count data, whilst also recording the area of river netted off for sampling. These data provided an estimate of survey effort, which was incorporated in the models as an offset (Zuur et al., 2009). To account for the hierarchical nature of the data, with sites nested in rivers, and to accommodate the distribution of the response data, GLMMs were employed to quantify the effect of flow reduction on brown trout abundance. This approach accounted for the degree of dependency in repeated measures and the nested structure of the data. Mixed models also allow generalised inferences to be made on a wider, but similar, population of sites and rivers beyond those for which data were collected. In this case, rivers downstream of reservoirs in Northern England that support brown trout populations.

The Before-After Control-Impact (BACI) model

The starting point was to follow the design of the original EA analysis in 2006 and fit a model to the abundance of spring season 1+ brown trout within a BACI design using data from 2000 to 2005 inclusive. This was modelled using a Poisson GLMM with random intercept at survey site level that took the form:

$$Count_{hijk} \sim Poisson(\mu_{hijk})$$

$$E[Count_{hijk}] = \mu_{hijk}$$

$$\text{var}(Count_{hijk}) = \mu_{hijk}$$

$$\log(\mu_{hijk}) = \eta_{hijk}$$

$Count_{hijk}$ = the kth count of brown trout from period h in river i at site j

where: period h = 1…2

river i = 1…4

site j = 1…12

count k = 1…66

$$\eta_{hijk} \sim \beta_1 + \beta_2 \text{ x } Period_h + \beta_3 \text{ x } River_i + \beta_4 \text{ x } Period_h \text{ x } River_i + offset\ (LSurv_{hijk})$$

$$a_j = N(0, \sigma^2)$$

where η_{hijk} contains main terms (Period, River) and one interaction term (Period x River) and an offset (log of fish survey area for each observation). The offset is used in count models to accommodate variation in the sampling effort that produced the count used in the response variable.

Period = 2 level factor (before or after flow cessation)

River = 4 level factor (Bradshaw Brook, River Bollin, River Goyt, River Sett)

Model parameters were estimated in a Bayesian framework (**Chapter 2**) using JAGS (Plummer, 2003) and the *R2jags* package (Su and Yajima, 2012) in the R statistical

environment (R Development Core Team, 2016). Three independent Markov chains were run simultaneously for each parameter with a burn-in of 5,000, thinning rate of 10 and 40,000 iterations, which resulted in 12,000 Markov Chain samples for each estimated parameter. Mixing (stationarity) and autocorrelation of chains were checked visually using trace plots and the Gelman-Rubin statistic (Brooks and Gelman, 1998). Autocorrelation was low and convergence was achieved in each case.

The model underwent validation to assess if assumptions for such a model were met. Critically, since the response variable was a count, the primary check was whether assumptions for dispersion were met. To check this the model was also used to simulate data using the Poisson distribution within the JAGS model-fitting process. This procedure allowed the fitted values for the model using the actual survey data to be compared with the fitted values for the simulated Poisson distributed data. Probability values were used for each data point to assess dispersion. Probability values of close to 0.5 indicate that the Poisson distribution is suitable and over-dispersion is absent. Values close to 0 or 1 indicate over-dispersion associated with an inappropriate distribution used in the model or other model mis-specification (Zuur et al., 2013). Probability values for the Poisson model were close to 0 and 1 so did not support the use of a Poisson GLMM.

A Negative Binomial GLMM was then fitted to the data with the counts of 1+ trout as the response variable and a log-link function between the response predictor function containing the explanatory variables. Models were structured as:

$$Count_{hijk} \sim NegBin(\mu_{hijk}, \theta)$$

$E[Count_{hijk}] = \mu_{hijk}$

$\text{var}(Count_{hijk}) = \mu_{hijk} + (\mu_{hijk}^2 / \theta)$

(θ = dispersion parameter for highly variable data, such as counts)

$Count_{hijk}$ = the kth count of brown trout from period h in river i at site j

where: period $h = 1 \ldots 2$

river $i = 1 \ldots 4$

site $j = 1 \ldots 12$

count $k = 1 \ldots 66$

$\eta_{hijk} \sim \beta_1 + \beta_2 \text{ x } Period_h + \beta_3 \text{ x } River_i + \beta_4 \text{ x } Period_h \text{ x } River_i + offset\ (LSurv_{hijk})$

$a_j = N(0, \sigma^2)$

see η_{hijk} for the Poisson GLMM (described above) for explanation of model terms.

The negative binomial GLMM contained the same paramaters, random effects and number of observations as the Poisson GLMM and was fitted with the same response variables (counts of 1+ trout). Model parameters were estimated using the same framework as the Poisson GLMM described above using JAGS and the *R2jags* package within the R statistical environment. Three independent Markov chains were run simultaneously for each parameter with a burn-in of 5,000, thinning rate of 10 and 40,000 iterations, which resulted in 12,000 Markov Chain samples for each estimated parameter as per the Poisson GLMM. Mixing (stationarity) and autocorrelation of

chains were checked visually using trace plots and the Gelman-Rubin statistic. Autocorrelation was low and convergence was achieved in each case.

To assess dispersion the negative binomial model was also used to simulate data using the same procedure as for the Poisson GLMM, this time using the negative binomial distribution within the JAGS model-fitting process. Probability values for the 1+ BACI model were 0.67 and support the use of negative binomial GLMMs. Further model validation showed no evidence of heterogeneity, non-linear patterns or spatial correlation in the model residuals (Zuur et al., 2013).

The goodness of fit for the models was assessed using an 'out of sample' prediction method (see Zuur et al., 2014 & Lunn et al., 2013 for examples and technical explanations). To apply the out of sample technique 20% of the raw data are randomly omitted and the models fitted to the remaining 80% of the data. The posterior mean distribution of the count of salmon and trout are then estimated from the model using the explanatory covariate values from the omitted 20% of data. The estimated posterior mean distribution of counts is then compared with the actual observed counts of salmon and trout to see if the observed value is within the estimated posterior distribution. The closer an observed value is to the centre of the posterior mean distribution of predicted counts suggests that the model has good predictive capability and fits observed data well. The results of the out of sample method are given in **figure 18**. The spring 1+ BACI model had 67% of observed counts within the estimated posterior mean distribution.

The before flow cessation period (*Before*) comprised data from the years 2000 to 2004 inclusive. Within the BACI design and associated statistical model the abundance of

brown trout in the before period was an average abundance from those five survey years. The flow cessation event took place in December 2004, which was between the fish survey periods of autumn 2004 and spring 2005. Fish surveys from spring 2005 onwards took place after the flow cessation event so the abundance of brown trout in the after period was an average abundance of all survey years within that period. The EA analysis and prosecution took place in 2006 so only included data from 2005 to cover the after period. Evidence for an impact of flow cessation, therefore, relied on a single year of data following the event compared with the average of five years of data in the before period. The inter-annual abundance of fish species such as brown trout is known to be highly variable (Elliott, 1995). As such, a BACI design that relied on a single year of data in the after period that was compared to the average of five years of data in the before period, could produce a potentially spurious interpretation of impact due purely to inter-annual variability in trout abundance.

Models accounting for inter-annual variation

In addition to fitting Bayesian GLMMs to data used in the original EA prosecution, models were fitted to data from 2000 to 2010 inclusive using each year as a factor. This approach permitted an investigation of the possibility that a solitary year of data in 2005 could influence the outcome of the BACI design, by examining whether the abundance of spring 1+ brown trout for that year was unusually low when with the abundance of spring 1+ from other years, before and after the year of the flow incident, across all rivers. This approach was also applied to data for other available age classes (0+ and 2+) and for both spring and autumn seasons in order to quantify the magnitude of flow impact on the wider brown trout populations and the likely duration of any impact. In

each case the abundance of brown trout was first modelled using Poisson GLMM with random intercept at survey site level but over-dispersion meant that a negative binomial GLMM would be required as in previous datasets. The fitted models took the form:

$Count_{hijk} \sim NegBin(\mu_{hijk}, \theta)$

$E[Count_{hijk}] = \mu_{hijk}$

$\text{var}(Count_{hijk}) = \mu_{hijk} + (\mu_{hijk}^2 / \theta)$

(θ = dispersion parameter for highly variable data, such as counts)

$Count_{hijk}$ = the kth count of brown trout from year h in river i at site j

where: year h = 1…11

river i = 1…4

site j = 1…12

count k = 1…111

$\eta_{hijk} \sim \beta_1 + \beta_2 \text{ x } Year_h + \beta_3 \text{ x } River_i + \beta_4 \text{ x } Year_h \text{ x } River_i + offset\ (LSurv_{hijk})$

$a_j = N(0, \sigma^2)$

where η_{hijk} contains main terms (Year, River) and one interaction term (Year x River) and an offset (log of fish survey area for each observation). The offset is used in count models to accommodate variation in the sampling effort that produced the count used in the response variable.

Year = 11 level factor (years 2000 to 2010 incl)

River = 4 level factor (Bradshaw Brook, River Bollin, River Goyt, River Sett)

In total six models were fitted with the following response variables:

1. Abundance of spring 0+ trout
2. Abundance of autumn 0+ trout
3. Abundance of spring 1+ trout
4. Abundance of autumn 1+ trout
5. Abundance of spring 2+ trout
6. Abundance of autumn 2+ trout

To draw inferences about model parameters a Bayesian approach was used (**Chapter 2**). A Bayesian GLMM is robust in dealing with relatively complex datasets like the one in the present study, specifically unbalanced nested data, an inherent lack of dependency due to repeated measures at sampling sites, and a highly varied non-normal response variable (fish counts). Bayesian models are flexible in allowing the estimation of a posterior distribution of differences between parameters and across levels of factors (Zuur et al., 2014; Kruschke, 2015). Notwithstanding these points, more general reservations have been raised in using null hypothesis significance testing, and particularly over the reliability of probability estimates in complex ecological models (Burnham and Anderson, 2014).

Diffuse or non-informative normal priors were put on all parameters. The model was fitted in a Bayesian framework using Markov Chain Monte Carlo (MCMC) with the *R2jags* package (Su and Yajima, 2012) in the R statistical environment (R

Development Core Team, 2016). Three independent Markov chains were run simultaneously. A burn-in of 5,000, thinning rate of 10 and 10,000 iterations were used and then updated to 40,000 iterations with the same thinning rate resulting in 12,000 iterations for each chain. Mixing (stationarity) and autocorrelation of chains were checked visually using trace plots and the Gelman-Rubin statistic (Brooks and Gelman, 1998). Autocorrelation was low and convergence was achieved in each case. Model validation showed no evidence of overdispersion, heterogeneity or non-linear patterns in the model residuals (Zuur et al., 2013). To assess dispersion the negative binomial model was also used to simulate data within the JAGS model-fitting process. Probability values for all models model ranged between 0.45 and 0.64 and supported the use of negative binomial GLMMs. Further model validation showed no evidence of heterogeneity, non-linear patterns or spatial correlation in the model residuals (Zuur et al., 2013).

The goodness of fit for the models was assessed using the same 'out of sample' prediction method used for the 1+ spring BACI model. The results of the out of sample method are given similar for the year models are similar to those obtained for the 1+ BACI model with between 48% and 66% of observed counts within the estimated posterior mean distribution of the year models.

RESULTS

Model results

BACI model for spring 1+ trout up to 2005

A clear reduction in spring 1+ brown trout density was observed in Bradshaw Brook in the period immediately following the flow cessation event in December 2004 (**Figure 6**). Posterior mean density of spring 1+ trout in Bradshaw Brook (**Table 4**) decreased by 85% from 0.040 to 0.006 trout m^{-2}. The three control rivers (Rivers Bollin, Goyt and Sett) also showed reductions in spring 1+ trout densities in the same period, ranging from 2.6% to 42.9% (**Table 4** and **Figure 6**). Despite all rivers showing a decrease the greatest posterior mean reduction occurred at Bradshaw Brook, which was almost twice the reduction observed for the River Bollin (42.9%) suggesting an abnormally low brown trout density for Bradshaw Brook in spring 2005.

The before – after event change in posterior mean site trout density for Bradshaw Brook represented a posterior mean reduction of 0.035 trout m^{-2} with 95% certainty that this reduction was between 0.021 and 0.055 trout m^{-2} (**Table 5** and **Figure 7**), which represented a reduction of between 80.8% and 88.7%. A similar reduction in posterior mean density (0.033 trout m^{-2}) was observed at the control River Bollin, but this had an upper credible interval containing zero, indicating no change in mean trout density for this river (**Table 5** and **Figure 7**). The observed reduction in posterior mean site density for the control River Goyt was 0.035 trout m^{-2} but, again, with zero in the upper credible interval suggesting no change. A reduction of 0.004 trout m^{-2} was observed for the River Sett, essentially a zero mean change in posterior mean site density although the credible interval for the mean change was noticeably wider than

that for other rivers indicating more variability in trout density between survey sites for this river.

Differences in the before period posterior mean site density between Bradshaw Brook and the controls rivers Bollin and Goyt were broadly similar, encompassing zeros in the 95% credible intervals (**Table 6** and **Figure 8**). Before period posterior mean site trout density was clearly lower in the Bradshaw Brook than the control River Sett by 0.111 trout m^{-2} (**Table 6** and **Figure 8**) despite wide credible intervals. This outcome implies that this control river, without a headwater reservoir, had consistently higher posterior mean site densities than Bradshaw Brook in the before period despite having greater variability in posterior mean site density. The two control Rivers Bollin and Goyt, which have headwater reservoirs, appeared to have broadly similar differences in their lower posterior mean site densities compared with the River Sett, although these were unclear due to zero in the upper credible intervals (**Figure 8**). The greater variability in posterior mean site density for the River Sett compared with the other controls rivers is notable and implies some association between a lack of headwater reservoir with greater flow variability and greater variability in mean site trout density.

The posterior mean site density of spring 1+ trout for the Bradshaw Brook in the period after flow cessation (**Table 7** and **Figure 9**) was clearly lower than that of all the control rivers. The posterior mean site density for the impacted river was 0.038, 0.033 and 0.142 trout m^{-2}, less than that for the Rivers Bollin, Goyt and Sett respectively. The clearly larger difference for the Sett is noteworthy, although there is much greater variability around this estimate, which was related to the greater variability in posterior mean site density for the Sett.

Differences in the posterior mean site density of spring 1+ trout among control rivers in the after period all contain zero in the credible intervals indicating no difference (**Table 7** and **Figure 9**). However, posterior mean site densities for the Rivers Bollin and Goyt appear to be marginally lower than that for the River Sett, again suggesting that this river, without a reservoir at its headwaters, supported marginally higher but more variable trout densities than the other controls with reservoirs in their headwaters.

When all results from this BACI model are considered together they indicate that densities of spring 1+ trout in the Bradshaw Brook, in the period immediately after the flow cessation event (2005 in this instance), clearly declined to a lower level than the before period (2000 to 2004) for this river. The reduction in posterior mean site trout density between periods was clear for Bradshaw Brook while changes at the controls rivers were effectively zero. Posterior mean site densities declined in the after period to a lower level than all the control rivers for the same period, despite having similar densities to two controls with reservoirs (Bollin and Goyt) in the before period. Results for the River Sett suggest that posterior mean site density of 1+ trout is generally higher, but more variable, in the absence of a reservoir in the headwaters and associated more natural flow variability.

Year model for spring 1+ trout (2000 - 2010)

An observable reduction in the posterior mean site density of spring 1+ trout was detected for Bradshaw Brook in 2005 compared with all other years, a marked pattern for this river when compared with that for the control rivers (**Figure 10**). When the posterior mean site density of 1+ trout for Bradshaw Brook in 2005 is compared with

the other years for this river it is clearly lower than all years (**Table 8** and **Figure 11**) suggesting that posterior mean site density in 2005 was exceptionally low. The posterior mean site density of spring 1+ in 2006 appears to be comparable with most years pre and post 2005, implying that low river flow conditions did not persist for long enough to affect the density of 1+ cohorts for 2006 onwards. When the general temporal pattern of posterior mean site density for Bradshaw Brook is compared with that for the control rivers (**Figure 10**) there appears to be a common reduction in 2005 for all rivers, although for the controls the reduction in that year was unlikely to represent a clear change due to the magnitude of credible intervals. Again, this result suggests that the reduction in 2005 for Bradshaw Brook was more extreme than for the other rivers and appears to support both my own BACI model results and the original EA analysis.

Year model for autumn 1+ trout (2000 - 2010)

There was no apparent difference between posterior mean site density of autumn 1+ trout for Bradshaw Brook in 2005 and most other years for that river (**Figure 12**). All rivers other than the Sett appeared to have a common reduction in posterior mean site density in 2005, the Sett appeared to have a similar posterior mean site density in 2005 to the previous year of 2004. When the posterior mean site density for autumn 2005 is compared with the autumn densities from other years at Bradshaw Brook (**Table 9** and **Figure 13**) there were only clear differences in four out of the nine years. Two of these years (2001 and 2004) were from the before cessation period while the remaining two years (2009 and 2010) were from the after cessation period. Indeed, the pattern in the after period (2005 to 2010) showed a general increase in density through time. Overall the results of this model suggest that there were no clear impacts from flow cessation on

autumn 1+ trout in Bradshaw Brook and that any impact was marginal and did not persist beyond spring 2005 for the 2005 1+ cohort.

Year models for spring and autumn 0+ trout (2000 - 2010)

The posterior mean site abundance of spring 0+ trout for Bradshaw Brook increased between 2004 and 2005 (**Figure 14**) and the abundance in 2005 was clearly no different to years 2003 and 2006 to 2010. The inter-annual variation in spring 0+ abundance for Bradshaw Brook appears to be similar to that for two of the three control rivers (Bollin and Sett). Abundance for the River Goyt shows a less variable pattern.

An increase in the posterior mean site abundance of autumn 0+ trout between 2004 and 2005 was observed for Bradshaw Brook and all control rivers (**Figure 15**), although for the rivers Goyt and Sett the credible intervals indicate no change since they are of similar magnitude in both those years and others. Between 2005 and 2006 all the control rivers showed a decrease in the posterior mean site abundance of autumn 0+ trout while Bradshaw Brook showed an increase. The magnitude and overlap of credible intervals for these years suggests that the observed pattern was of no clear change. Overall the results for both spring and autumn provide little or no evidence than flow cessation impacted the 0+ age class in either season in 2005.

Year models for spring and autumn 2+ trout (2000 - 2010)

Between 2004 and 2005 an increase in the posterior mean site abundance of spring 2+ trout was observed at Bradshaw Brook and all the controls (**Figure 16**), although the change at Bradshaw Brook appears to be clearer due to the smaller credible intervals. This result suggests that the posterior mean site abundance of spring 2+ trout at the flow

impacted Bradshaw Brook increased following flow cessation while little or no change was observed at the control rivers. A similar, but less marked pattern was observed for the posterior mean site abundance of autumn 2+ trout (**Figure 17**). Overall these combined results provide no evidence to suggest that flow cessation in December 2004 impacted the abundance of 2+ trout in 2005.

The 2+ results can also be used to test for lasting impacts on the spring 1+ cohort of 2005, where both the BACI and year models for this cohort suggest there were clear reductions in their abundance in 2005. Trout that were in the 1+ age class in 2005 would be in the 2+ age class in 2006 and so any impacts in 2005 could be predicted to have an effect on the abundance of 2+ trout in 2006. When the posterior mean site abundance of 2+ trout for Bradshaw Brook are considered in spring and autumn of 2006 (**Figures 16** and **17**) there is no clear reduction when compared with other years. This finding suggests that despite the observed reductions in posterior mean site trout abundance for the 2005 spring 1+ cohort at Bradshaw Brook, there is no evidence to show that this cohort was affected by the flow cessation in subsequent years.

DISCUSSION

The aim of this study was to fit statistical models to a dataset used qualitatively by the Environment Agency as part of their prosecution of a water company for accidentally stopping river flows with a presumed impact on a brown trout population in Bradshaw Brook. I fitted models that not only quantified the magnitude and duration of impact but that also better accounted for the distribution of the response variable (fish counts), the nested structure of the data and associated dependency due to repeated measures at multiple survey sites within each river. An important part of my aim was to use

Bayesian inference so that direct statements about the probability of estimated model parameters and predictions of impact could be made. I applied a BACI approach and also an approach that quantified inter-annual variability in spring 1+ trout density for the years 2000 to 2005 and then compared these results with additional years of data, a luxury unavailable to the EA at the time of their analysis and prosecution of the water company. My objectives were to set the impact detected in 2005 on spring 1+ trout against the longer time series for that age class. I also applied my analyses to other age classes and seasons to quantify the evidence that the 2004 flow cessation on Bradshaw Brook represented an important impact for the wider trout population of the river.

The BACI model not only supported the overall conclusion of the EA prosecution, that spring 1+ trout density was impacted in the after flow cessation period at Bradshaw Brook, it also estimated the density reduction with 95% certainty, given the data. However, a limitation and potential criticism is that this approach compared one year of data for the after flow cessation period (2005) with an average from four years of data for the before period (2000 to 2004). Addressing this question was the main purpose of fitting the year models. The year model for spring 1+ estimated posterior mean site density in 2005 compared with other years at Bradshaw Brook and showed that 2005 clearly had an unusually low posterior mean site density compared with the other years. This outcome was not observed at any of the control rivers and implies a causal link between the observed densities in 2005 at Bradshaw Brook and the flow cessation event.

The results of year models for autumn 1+, spring and autumn 0+, and spring and autumn 2+ trout did not concur with the results for spring 1+ trout. In terms of evidence of an impact on the brown trout population of Bradshaw Brook, these results imply that

there was an acute but short-lived impact, termed a 'pulse' impact (Downes et al., 2002), on a specific age class within a specific year followed by rapid recovery.

The flow incident of December 2004 on Bradshaw Brook is similar in character to dewatering events associated with hydropeaking from hydropower generation due to a rapid decrease in flow of short duration (**Chapter 1**; Saltveit et al., 2001). Hydropeaking occurs when hydropower schemes are activated in response to increased demand for electricity, resulting in rapidly increased river flow downstream of the scheme, then deactivated once demand has passed, resulting in rapidly decreased river flow. The latter is associated with fish stranding and is seen as a key impact on fish populations inhabiting rivers downstream of hydropower schemes. The causes (natural and anthropogenic) and effects of fish stranding are reviewed in Nagrodski et al. (2012) and show that 80% of stranding incidents relate to anthropogenic causes and of these over 60% are associated with hydropower. Fish mortality associated with stranding is the most striking result, but less is known about the sub-lethal and long-term consequences of flow cessation on fish populations (Nagrodski et al., 2012). In this situation fish are restricted to sub-optimal habitat, or away from their preferred habitat, when flows are rapidly decreased, a situation that is likely to have occurred at Bradshaw Brook for a short interval (6 – 12 hours) at least. As flow decreased in the river individuals are likely to have moved downstream away from the dewatered reaches. This seeking out of refugia is critical in natural situations such as drought and is critical to the persistence of populations in disturbed environments (Lake, 2003). Davey and Kelly (2007) monitored fish populations in a naturally intermittent stream in New Zealand and observed brown trout migrating to permanent water as occupied reaches dried out. They also showed that, once flows recovered, recolonisation rate decreased

with time, especially for trout. This finding suggests that trout have the capacity to rapidly recolonise once flow conditions recover, a response the data for autumn 1+ trout appear to show at Bradshaw Brook in 2005.

The flow incident occurred during winter 2004, a period when buried trout eggs are developing in the spawning gravels with the potential for dewatering to reduce egg survival rates (Casas-Mulet et al., 2014). Although egg mortality may have occurred, data on mortality rates were unavailable. Despite this effect any impact does not appear to have translated into effects on spring or autumn 0+ juveniles in 2005. Density dependence is a key control on the abundance of the earliest age classes of trout (Elliott, 1995), so despite any potential egg survival impacts, post emergence density dependence is likely to dampen those effects. The study of Casas-Mulet et al. (2014) in a Norwegian river showed that the main factors explaining egg mortality were the combination of dry conditions from dewatering and sub-zero temperatures.

My results, and those from other studies, suggest that brown trout populations can be resistant and resilient to short-term flow reductions, but this is likely to be conditional on the number, frequency and duration of dewatering events. In this instance my results suggest that the flow incident triggered a short-term response of 1+ trout to move to refugia then recolonised sites between seven to ten months after the incident. There was no evidence to suggest that other age classes (0+ and 2+) were affected, which implies that the 1+ trout cohort in 2005 was unaffected in the longer term, as demonstrated by the 2+ results. The 0+ results suggested that egg survival in the winter of 2004 was not affected by the dewatering event, or that any effects were regulated by density dependence acting on young of year in 2005. These results are important for fishery, river and water resources managers because they show that pulse

impacts, such as that on Bradshaw Brook, are unlikely to cause long-term detrimental effects in trout populations. However, complacency is to be guarded against since an increase in the number, frequency and duration of such events will increase the risk of longer-term effects. In order to be better prepared for such events and to improve our understanding of their population impacts, appropriately designed monitoring and application of the most appropriate and up-to-date statistical methods are required.

In addition to quantifying the magnitude and duration of the flow cessation impacts on trout in Bradshaw Brook, I also found evidence suggesting that densities of trout in a river without a reservoir in its headwaters are generally higher and more variable than those with headwater reservoirs. This finding implies that the presence of reservoirs can influence the overall abundance of trout and their temporal variability. The reservoirs in question have been in place since Victorian engineers in the 1800s built them to supply the growing population, industries and canal networks in the region. Therefore, it can be assumed that the current brown trout populations are a product of this long history of river alteration and management, and that their abundance in these rivers may have been higher pre-construction. To explore this idea further additional examples of upland rivers without reservoirs that support trout populations that could be monitored through time, along with appropriate controls, would be informative. An experimental approach to construct reservoirs could be used on rivers of interest combined with monitoring the temporal response of trout abundance could be used to directly ask how reservoir construction and management affects trout populations in the long-term, compared with locations where reservoir construction has not taken place.

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TABLES

Table 1. Summary of 0+ brown trout caught in electrofishing surveys for each river and year.

	Year											
River	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Total
Bradshaw	164	170	198	84	200	53	147	123	166	96	196	1597
Bollin	88	83	50	115	110	68	102	47	27	81	NA	771
Goyt	56	20	82	68	87	38	77	41	NA	37	80	586
Sett	27	53	151	89	148	109	54	40	NA	26	84	781
Total	335	326	481	356	545	268	380	251	193	240	360	3735

Table 2. Summary of 1+ brown trout caught in electrofishing surveys for each river and year.

	Year											
River	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Total
Bradshaw	164	170	198	84	200	53	147	123	166	96	196	1597
Bollin	88	83	50	115	110	68	102	47	27	81	NA	771
Goyt	56	20	82	68	87	38	77	41	NA	37	80	586
Sett	27	53	151	89	148	109	54	40	NA	26	84	781
Total	335	326	481	356	545	268	380	251	193	240	360	3735

Table 3. Summary of 2+ brown trout caught in electrofishing surveys for each river and year.

	Year											
River	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	Total
Bradshaw	35	138	108	67	37	110	57	78	73	83	51	837
Bollin	15	57	39	29	35	33	19	29	17	20	4	297
Goyt	24	46	50	65	51	62	33	25	NA	30	34	420
Sett	6	25	92	96	91	94	132	49	NA	50	62	697
Total	80	266	289	257	214	299	241	181	90	183	151	2251

Table 4. Posterior mean estimates of spring 1+ brown trout density (N m^{-2}) for each river and flow incident period (up to year 2005 inclusive). CrI is the 95% Bayesian credible interval.

River	Period	Posterior mean	Lower CrI	Upper CrI	% mean change
Bradshaw	Before	0.040	0.026	0.062	
	After	0.006	0.002	0.011	- 85.0
Bollin	Before	0.077	0.041	0.131	
	After	0.044	0.017	0.093	-42.9
Goyt	Before	0.057	0.026	0.110	
	After	0.039	0.012	0.097	-31.5
Sett	Before	0.151	0.070	0.289	
	After	0.147	0.052	0.357	-2.6

Table 5. Posterior mean estimates of the before and after flow incident change in spring 1+ brown trout density (N m^{-2}) for each river (up to year 2005 inclusive). CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold.

River	Posterior mean	Lower CrI	Upper CrI
Bradshaw	-0.035	**-0.055**	**-0.021**
Bollin	-0.033	-0.078	0.010
Goyt	-0.018	-0.064	0.032
Sett	-0.004	-0.127	0.170

Table 6. Posterior mean estimates of the differences in spring 1+ brown trout density (N m^{-2}) between the impacted river and control rivers in the before period. CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold.

Rivers	Posterior mean	Lower CrI	Upper CrI
Brad v Bollin	-0.037	-0.093	0.006
Brad v Goyt	-0.016	-0.071	0.021
Brad v Sett	-0.111	**-0.251**	**-0.026**
Bollin v Goyt	0.020	-0.043	0.081
Bollin v Sett	-0.074	-0.215	0.022
Goyt v Sett	-0.094	-0.238	0.003

Table 7. Posterior mean estimates of the differences in spring 1+ brown trout density (N m^{-2}) between the impacted river and control rivers, and between controls rivers, in the after period (year 2005 only). CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold.

Rivers	Posterior mean	Lower CrI	Upper CrI
Brad v Bollin	-0.038	**-0.087**	**-0.011**
Brad v Goyt	-0.033	**-0.092**	**-0.006**
Brad v Sett	-0.142	**-0.352**	**-0.046**
Boll v Goyt	0.005	-0.060	0.063
Boll v Sett	-0.104	-0.316	0.005
Goyt v Sett	-0.109	-0.321	0.004

Table 8. Posterior mean estimates of the differences in mean spring 1+ brown trout density (N m^{-2}) in 2005 versus all other years for Bradshaw Brook. CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold.

Year	Posterior mean	Lower CrI	Upper CrI
2000	-0.046	**-0.083**	**-0.021**
2001	-0.032	**-0.060**	**-0.014**
2002	-0.047	**-0.086**	**-0.022**
2003	-0.012	**-0.026**	**-0.002**
2004	-0.050	**-0.092**	**-0.025**
2006	-0.024	**-0.047**	**-0.010**
2007	-0.041	**-0.089**	**-0.015**
2008	-0.032	**-0.063**	**-0.013**
2009	-0.026	**-0.067**	**-0.006**
2010	-0.056	**-0.107**	**-0.026**

Table 9. Posterior mean estimates of the differences in autumn 1+ brown trout density (N m^{-2}) in 2005 versus all other years for Bradshaw Brook. CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold.

Year	Posterior mean	Lower CrI	Upper CrI
2001	-0.027	**-0.057**	**-0.004**
2002	-0.016	-0.040	0.002
2003	-0.002	-0.019	0.012
2004	-0.031	**-0.075**	**-0.003**
2006	-0.011	-0.033	0.005
2007	-0.014	-0.040	0.004
2008	-0.021	-0.052	0.000
2009	-0.049	**-0.109**	**-0.015**
2010	-0.078	**-0.189**	**-0.023**

FIGURES

Figure 1. Location of study sites in north-west England (indicated by red dots).

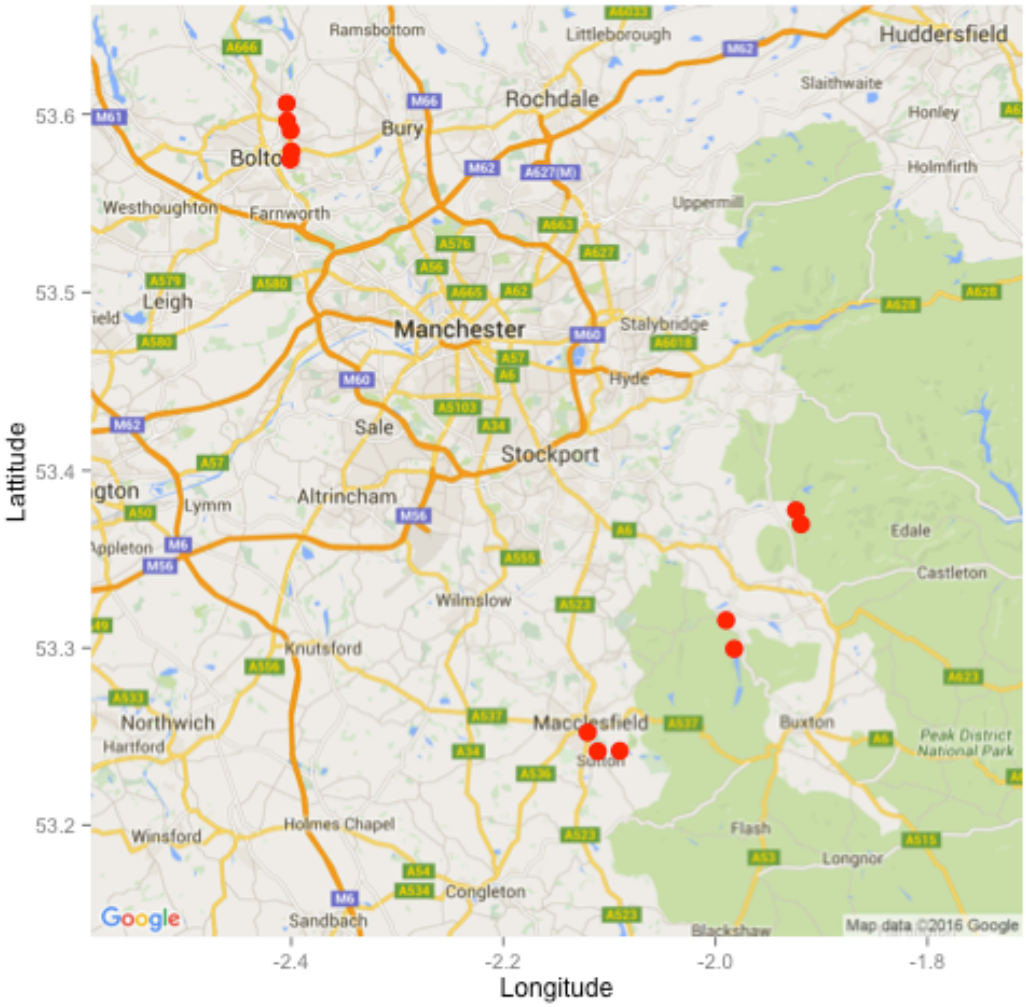


Figure 2. Location of sampling sites on the Bradshaw Brook (indicated by red dots).

Figure 3. Location of sampling sites on the River Bollin (indicated by red dots).

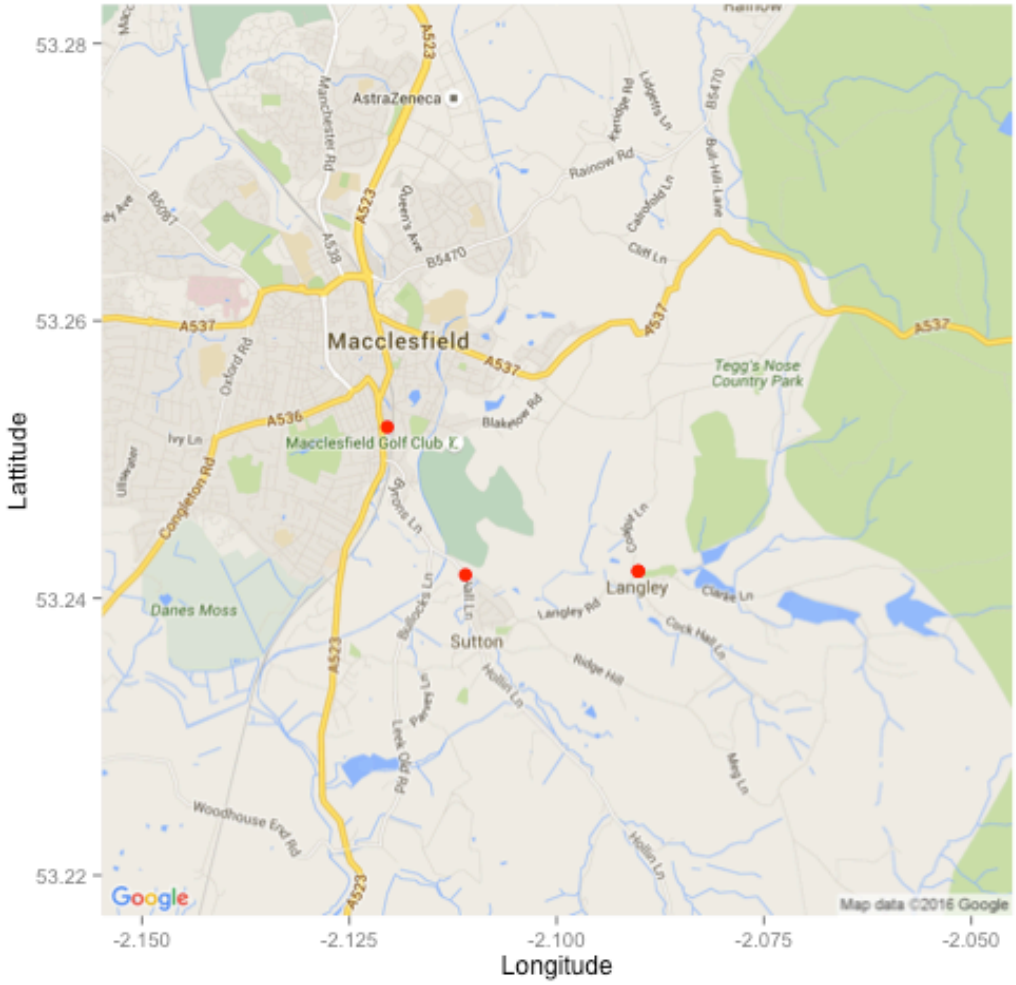


Figure 4. Location of sampling sites on the River Goyt (indicated by red dots).

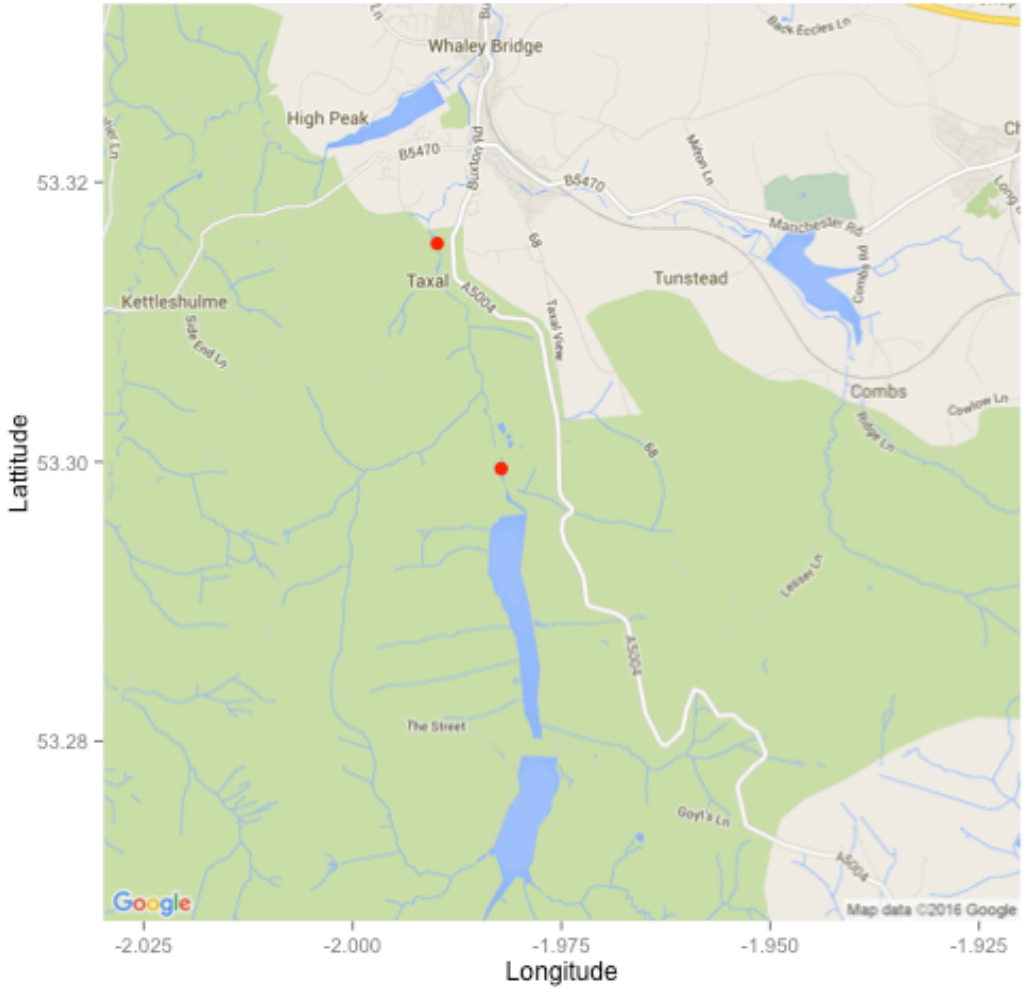


Figure 5. Location of sampling sites on the River Sett (indicated by red dots).

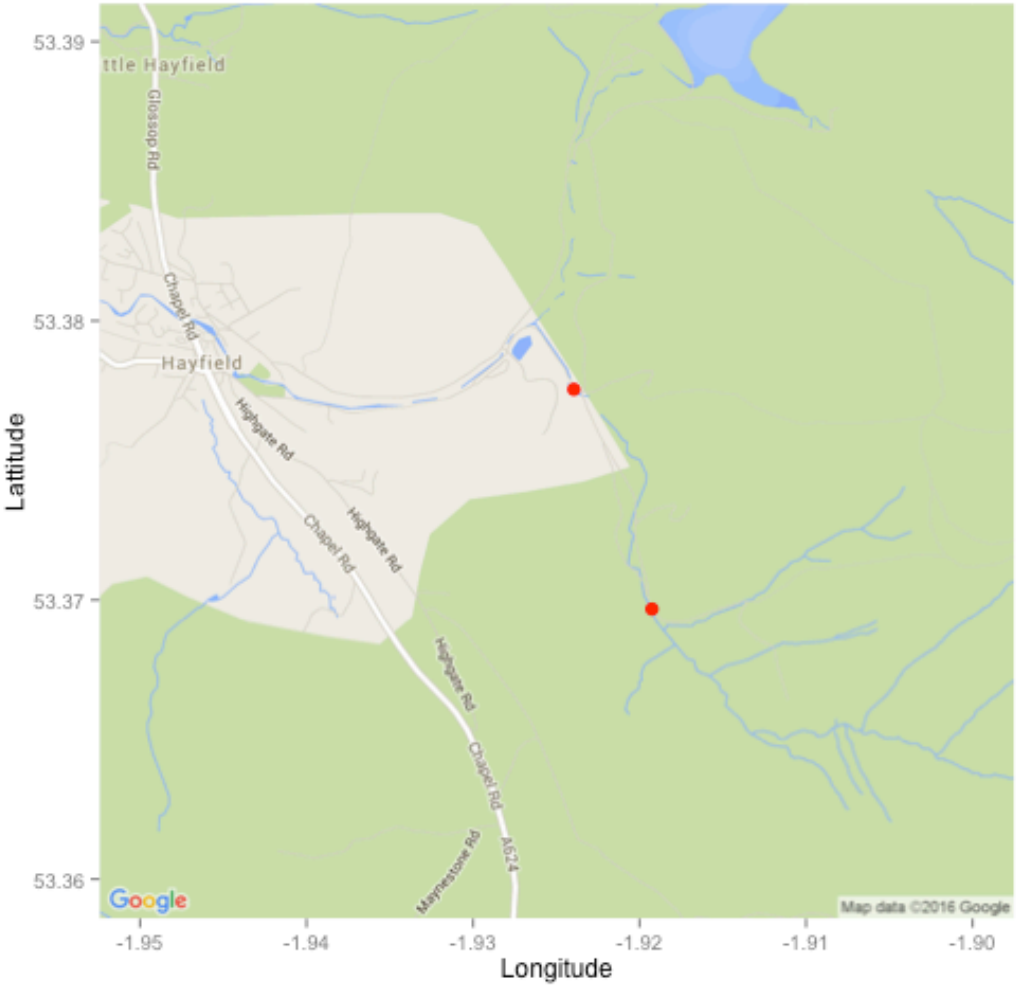


Figure 6. Estimated mean density of spring 1+ brown trout before and after flow incident (up to year 2005 inclusive). Open circles are control rivers, closed circles are impacted river. Vertical lines are Bayesian 95% credible intervals. Dashed lines show trajectory of density change between periods.

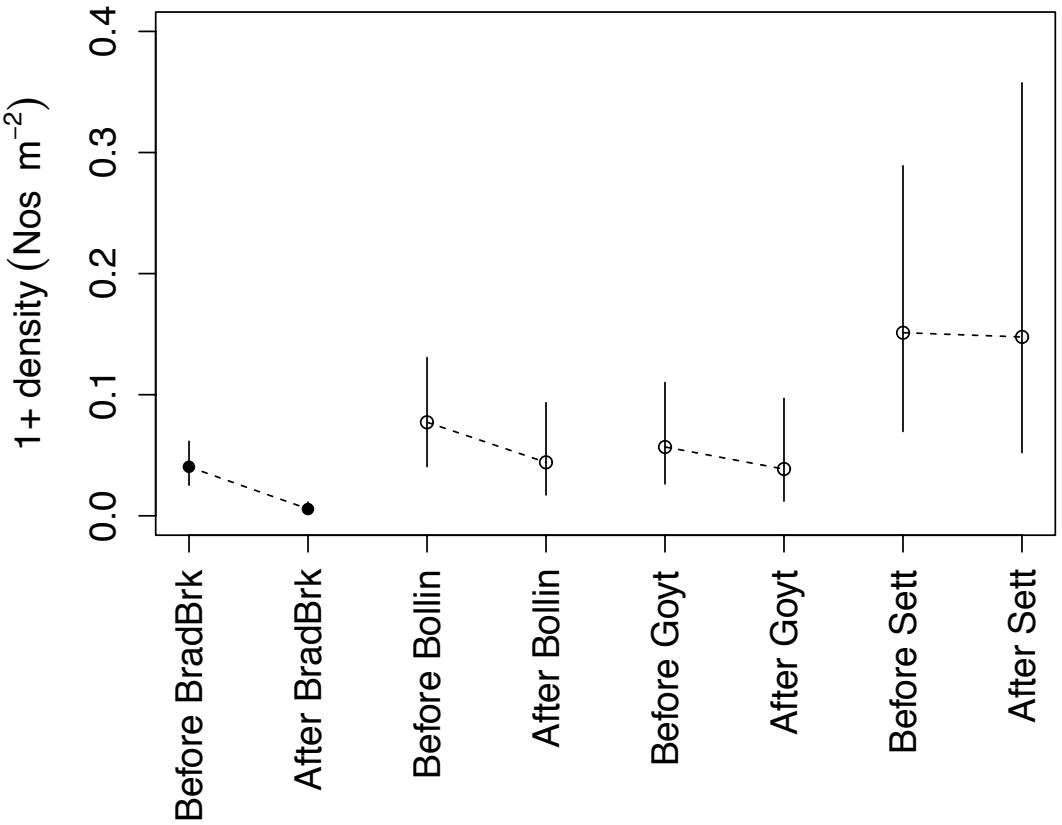


Figure 7. Estimated change in mean density of spring 1+ brown trout for each river before and after flow incident (up to year 2005 inclusive). Open circles are control rivers, closed circles are impacted river. Vertical lines are Bayesian 95% credible intervals. Horizontal line indicates zero change in mean density between periods. Horizontal line at zero indicates no change.

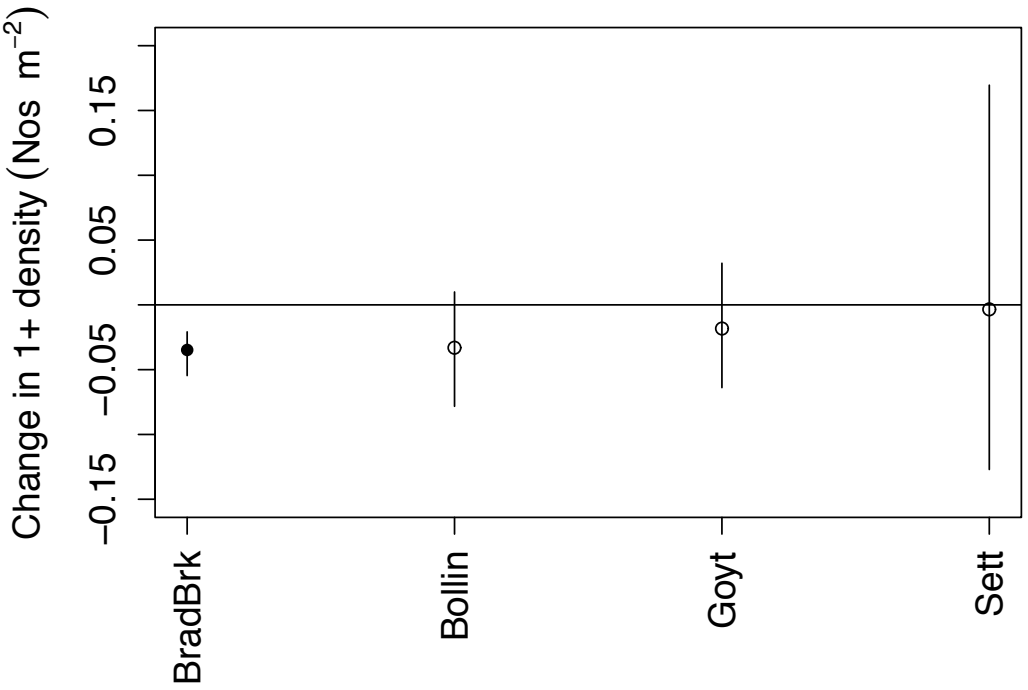


Figure 8. Difference in mean site density of spring 1+ brown trout comparing the impacted river and control rivers in the before period. Vertical lines are Bayesian 95% credible intervals. Horizontal line at zero indicates no change.

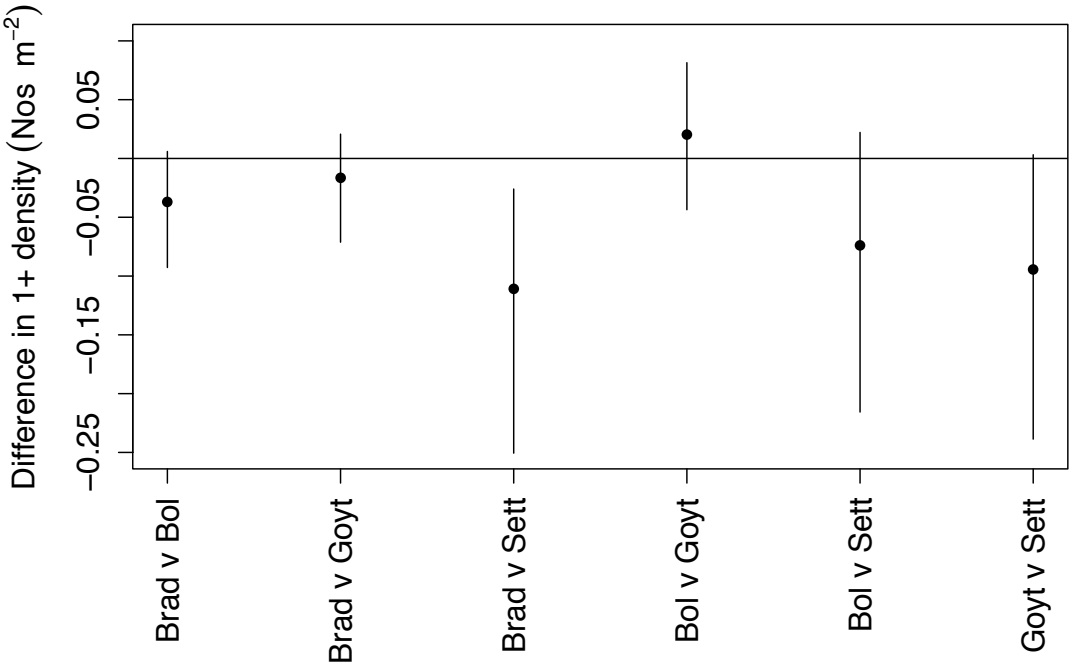


Figure 9. Difference in mean site density of spring 1+ trout between the impacted river and control rivers, and between control rivers, in the after period (2005). Vertical lines are Bayesian 95% credible intervals. Horizontal line at zero indicates no change.

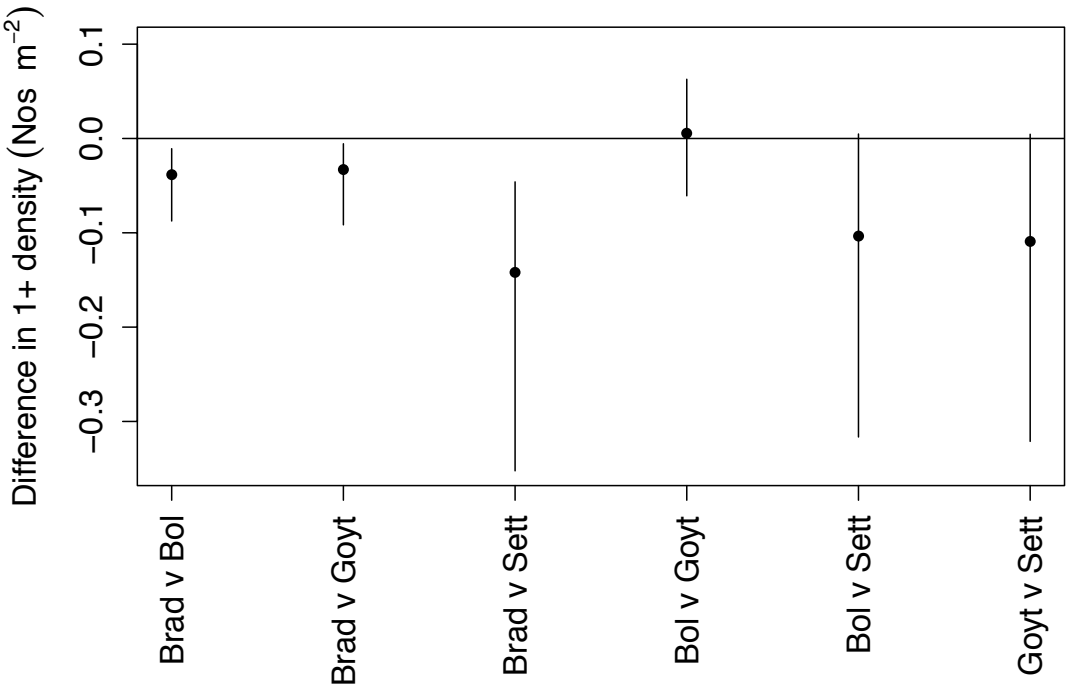


Figure 10. Estimated mean density of spring 1+ brown trout in each year. Closed circles are impacted year 2005. Vertical lines are Bayesian 95% credible intervals. Dashed lines show trajectory of density change between years. Note different trout density scale for each river.

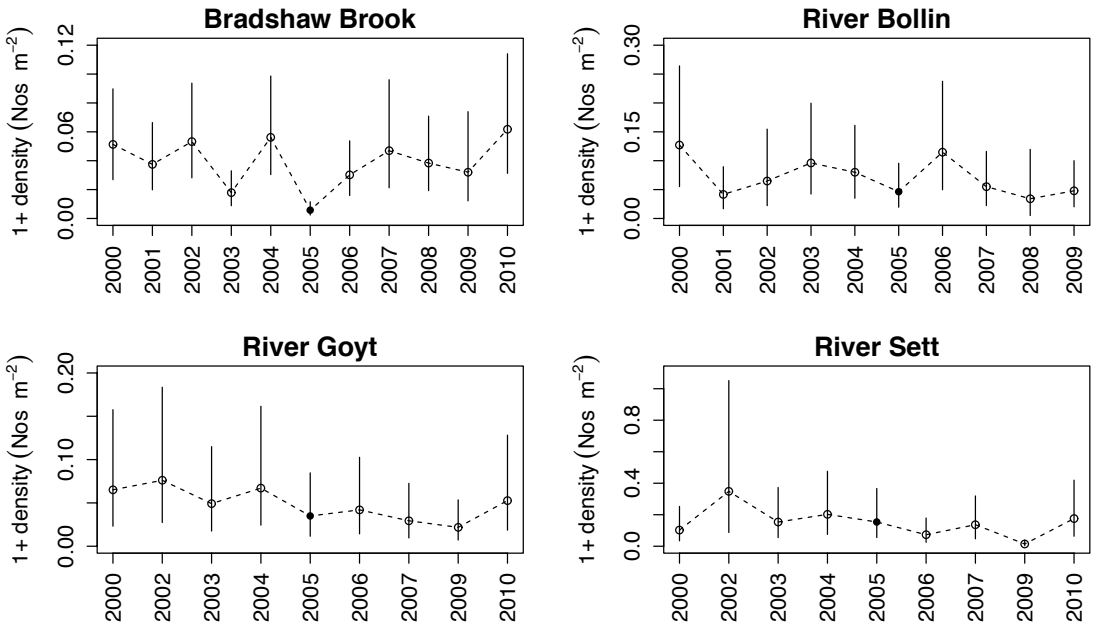


Figure 11. Differences in mean site density of spring 1+ trout in 2005 versus all other years for Bradshaw Brook. Vertical lines are Bayesian 95% credible intervals. Horizontal line at zero to indicate no difference.

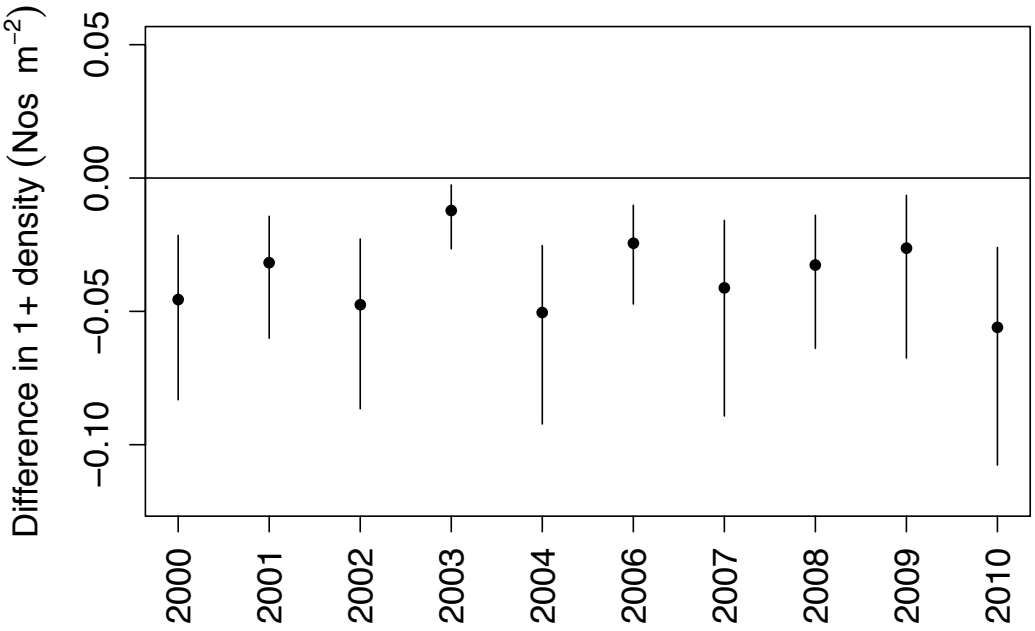


Figure 12. Estimated mean density of autumn 1+ brown trout per year. Closed circles are impacted year 2005. Vertical lines are Bayesian 95% credible intervals. Dashed lines show trajectory of density change between years. Note different trout density scale for each river.

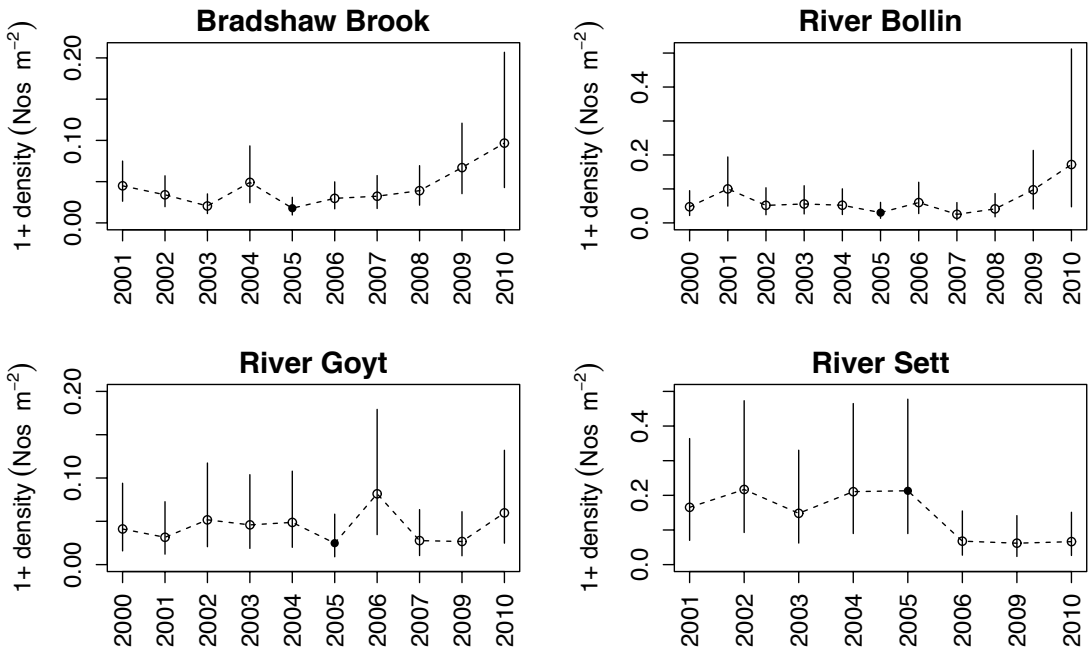


Figure 13. Differences in mean site density of autumn 1+ trout in 2005 versus all other years for Bradshaw Brook. Vertical lines are Bayesian 95% credible intervals. Horizontal line at zero to indicate no difference.

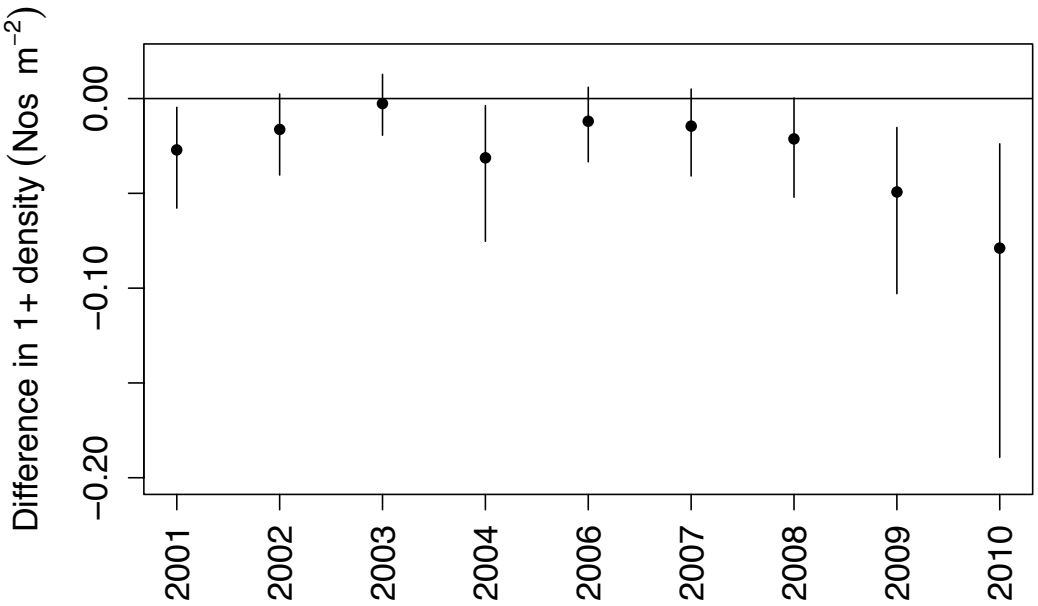


Figure 14. Estimated mean density of spring 0+ brown trout per year. Closed circles are impacted year 2005. Vertical lines are Bayesian 95% credible intervals. Dashed lines show trajectory of trout density change between years.

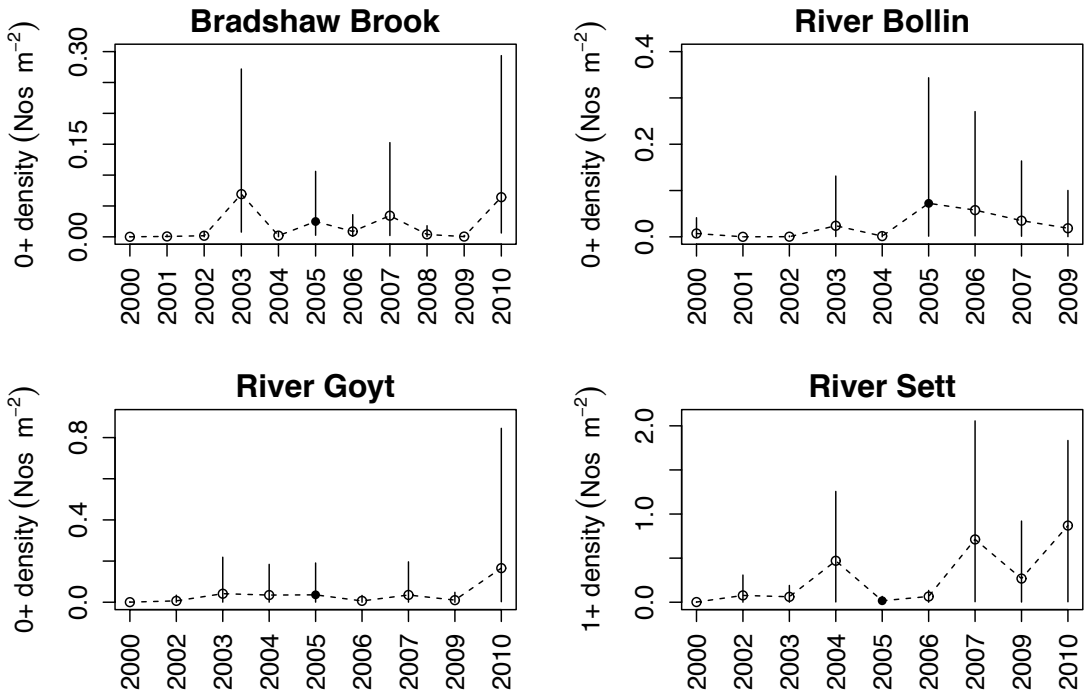


Figure 15. Estimated mean density of autumn 0+ brown trout per year. Closed circles are impacted year 2005. Vertical lines are Bayesian 95% credible intervals. Dashed lines show trajectory of trout density change between years.

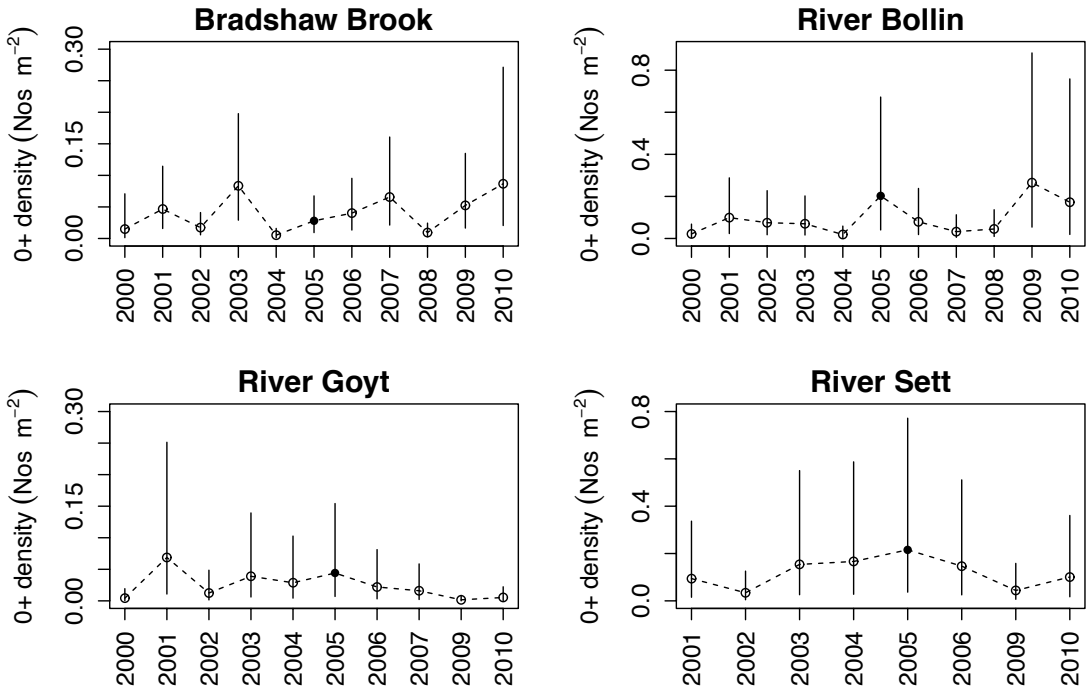


Figure 16. Estimated mean density of spring 2+ brown trout per year. Closed circles are impacted year 2005. Vertical lines are Bayesian 95% credible intervals. Dashed lines show trajectory of trout density change between years.

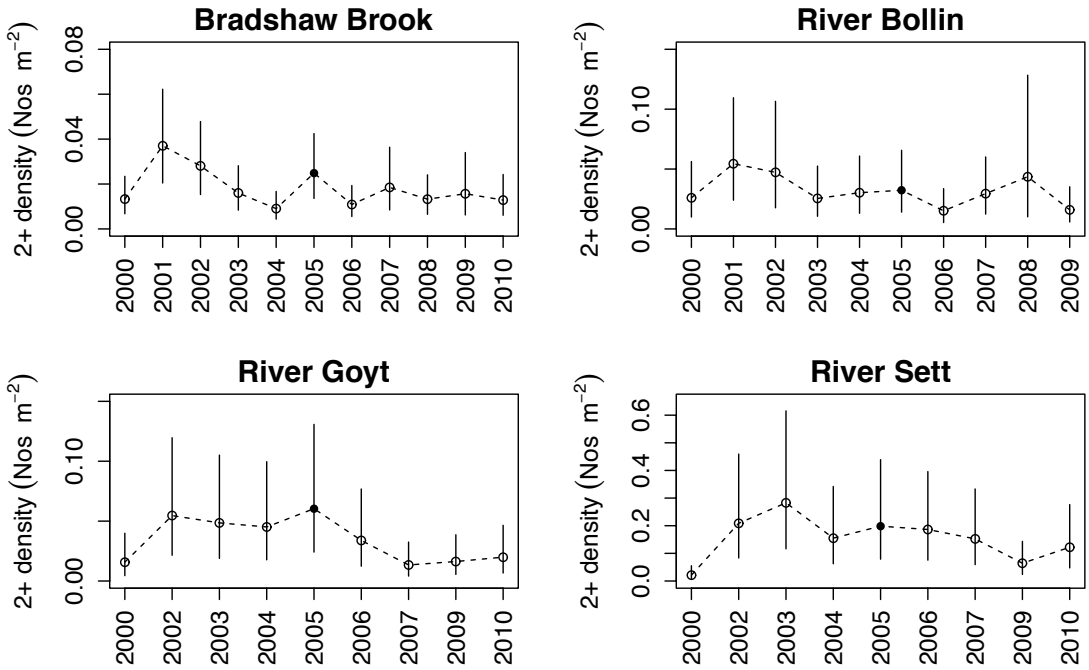


Figure 17. Estimated mean density of autumn 2+ brown trout per year. Closed circles are impacted year 2005. Vertical lines are Bayesian 95% credible intervals. Dashed lines show trajectory of trout density change between years.

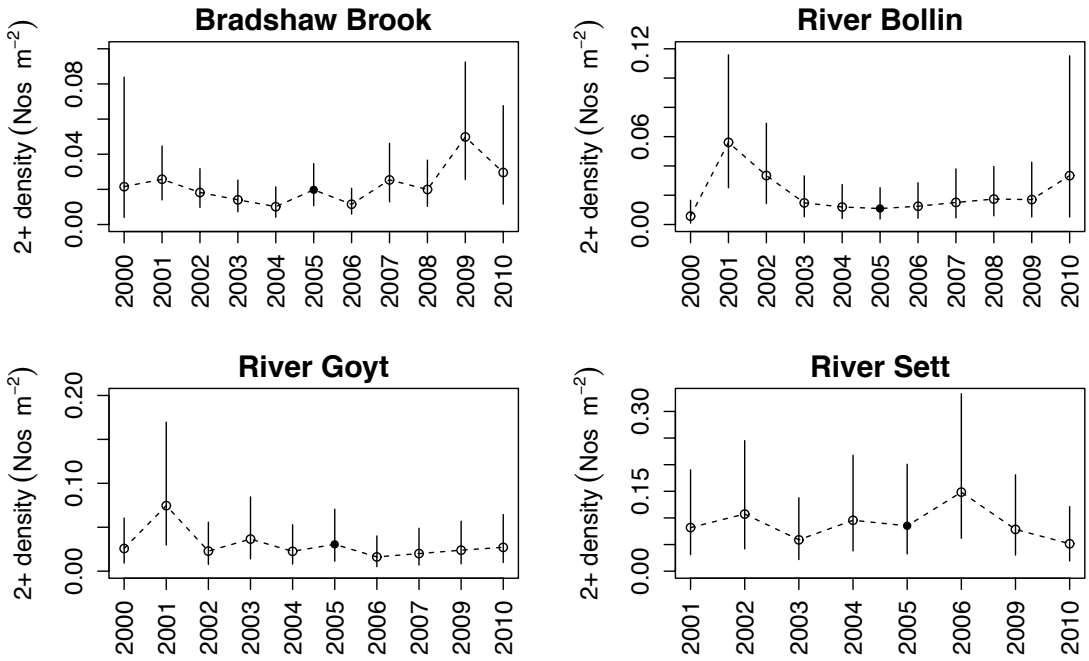
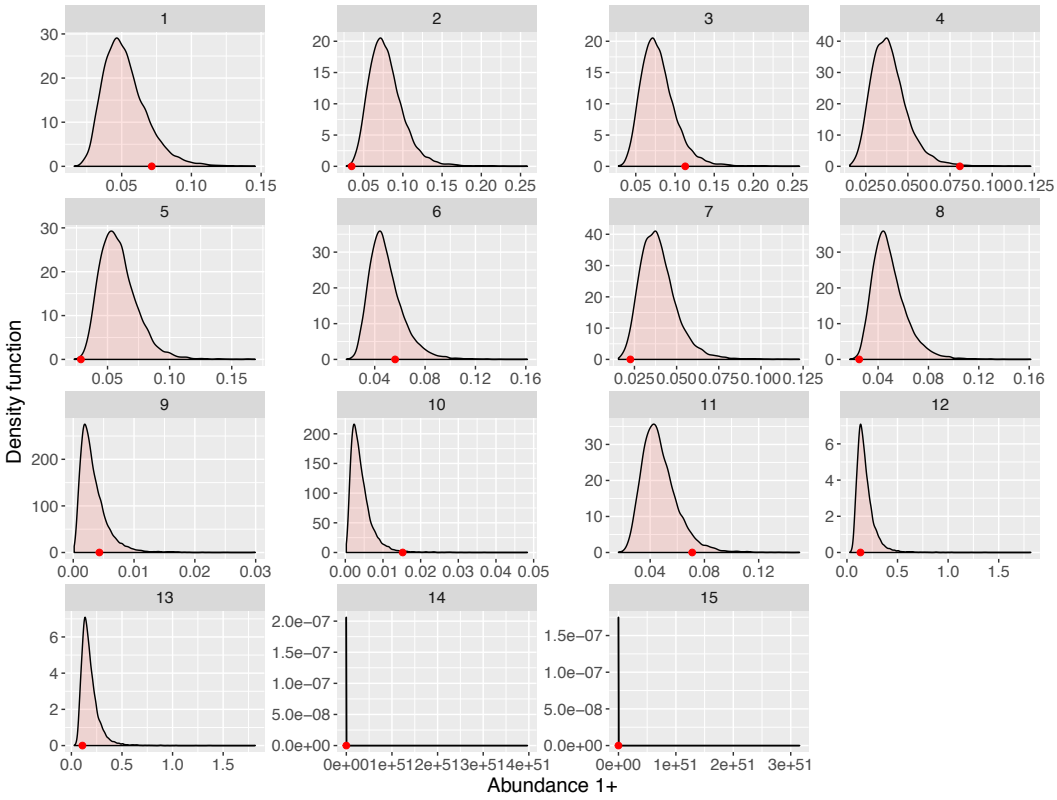


Figure 18. Out of sample prediction results for the 1+ BACI negative binomial model. Each panel represents one omitted count of 1+ trout. The posterior mean distribution obtained from the model is shown for each panel. The red dot is the actual omitted count.



Chapter Five

THE ABUNDANCE OF JUVENILE SALMONIDS IN RESPONSE TO RIVER FLOW RESTORATION

ABSTRACT

Human alterations to river flow are associated with loss of aquatic biodiversity. For salmonid fishes, flow is critical to support populations throughout all life history stages. I investigated the short-term effects of flow restoration on the over-summer survival of 0+ and 1+ brown trout (*Salmo trutta*) and Atlantic salmon (*S. salar*) in upland rivers in northern England that have historically experienced low summer flow as a result of impoundment and water abstraction. Four rivers were surveyed in a Before-After-Control-Impact (BACI) design, with two rivers undergoing summer flow restoration and two acting as controls. Summer and autumn electrofishing surveys were conducted on all rivers between 2011-2014. Flow restoration was implemented on the two restored rivers in 2012. Generalised linear mixed models (GLMMs) with Bayesian inference were used to test for the short-term effects of flow restoration on the over-summer survival of 0+ and 1+ salmonids. Evidence for important benefits of flow restoration for 0+ and 1+ salmonids at restored rivers in comparison with control sites was limited. A lack of clear benefits on flow-restored rivers may be linked to short-tem negative impacts of restoration works, small scale localised effects, the short time scale of monitoring or a lack of suitability of control rivers. The study highlights the necessity for a rigorous statistical approach to site selection and study design in order to assess the effectiveness of river flow restoration measures. River flow restoration studies often produce monitoring data that are unbalanced, have highly skewed non-normal response

variables and inherent dependency. I demonstrate the effectiveness of Bayesian GLMMs for analysing data from such studies. I discuss the implications of the results for water resources and river management.

INTRODUCTION

Water requirements for public supply, agriculture, industry and power generation, as well as activities associated with flood control, have led to major alterations to river flow and discharge regimes, with consequent ecological degradation and loss of aquatic biodiversity worldwide (Poff et al., 1997; Lytle and Poff, 2004; Warren et al., 2015; **Chapter 1**). River flow regimes potentially affect several key aquatic processes, such as levels of dissolved oxygen, sediment transport and deposition, water quality, and habitat type and distribution (Poff et al., 1997; Richter et al., 1998; Bunn and Arthington, 2002). River flow variation influences the spatial and temporal distribution of a broad range of aquatic biota including fish (Jowett et al., 2005; Poff and Zimmerman, 2010). Human perturbation of flow, either by directly extracting water, regulating rivers using weirs and dams, or indirectly by altering run-off through changing land use, can cause disruptions to fish populations and communities (Freeman et al., 2001; Cattanéo, 2005; Park et al., 2006; Benejam et al., 2010). Run-of-river intake weirs also prevent downstream sediment movement, which is important in providing river channel habitat for riverine biota, especially salmonid fishes (Poff et al., 1997; Pulg et al., 2013). Consequently, understanding the relationship between river flow and discharge, water abstraction and fish abundance and distribution represents a major goal for aquatic ecology and fisheries management, and particularly for river rehabilitation and restoration (Richter et al., 2003; Souchon et al., 2008; Poff et al., 2010). Because of

their significance for ecological, commercial and conservation reasons, salmonid fishes have been central in the debate over flow management for biodiversity (Beechie et al., 2006; Milner et al., 2012; Nislow and Armstrong, 2012; Warren et al., 2015).

While there is a pressing demand for rational management of freshwater resources, attempts to rehabilitate and restore aquatic habitats take a number of forms that vary widely in their effectiveness (reviewed by Roni et al., 2008). The emerging science of hydroecology attempts to understand and quantify the impacts of water resources management on aquatic biota. Ultimately a key goal is in deriving an understanding of how river flow management can be used as a river management and conservation tool. The term 'river flow' in this context is defined as river discharge; i.e. the volume of water passing a fixed point, such as a flow gauging station. This definition is standard terminology in river and water resources management. An important aspect of river management is the setting of environmental flows to maintain or enhance the ecological integrity of rivers (Poff et al., 1997; Tharme, 2003; Arthington et al., 2006). However, setting environmental flows is often undertaken with little or no reference to established relationships between river flow and biota, mainly because these relationships have yet to be fully characterised (Poff and Zimmerman, 2010; Poff et al., 2010).

To address perceived ecological problems arising from water abstraction and impoundments, the Environment Agency of England (EA) implemented a national Restoring Sustainable Abstraction (RSA) programme in the late 1990s. The basis to this programme is to identify water abstraction activities that impact, or pose an unacceptable risk, to aquatic ecology and designated sites and species. A main focus at the time of inception was to protect riverine Special Areas of Conservation (SAC) and

species designated under the EU Habitats Directive (92/43/EEC) and Sites of Special Scientific Interest (SSSI) designated under the Wildlife and Countryside Act 1981. More recently the remit has broadened to include meeting the EU Water Framework Directive (2000/60/EC) target of achieving 'Good Ecological Status'.

In the North West region of England, the EA undertook a multiple catchment RSA study with the water company United Utilities (UU) to quantify the ecological benefits of altering water abstraction and restoring river flow regimes to a less altered state. The intended beneficiaries of the study were riverine macroinvertebrates and salmonid fishes within the upper reaches of rivers designated as SAC and SSSI. For salmonids the early life stages (0+ and 1+ age classes) were targeted, since these are the most abundant age classes to measure recruitment, survival and production and are judged most susceptible to alterations in flow regime due to their limited capacity to move large distances (Environment Agency, 2009; Milner et al., 2012; Warren et al., 2015). These age classes represent the key freshwater life stages, with implications for the dynamics of both migratory and resident populations.

Measuring an ecological response to river flow alteration can be problematic to demonstrate and requires a specific experimental design paired with an appropriate statistical model. The Before-After-Control-Impact (BACI) design is one that is often employed, thereby controlling for temporal and spatial effects (Stewart-Oaten et al., 1986; Underwood, 1992; Smith, 2002; see **Chapter 4** for full consideration).

The goal of the present study was to use Bayesian GLMMs to assess the results of a 4-year controlled study focused on four rivers, two of which underwent flow restoration within the North West RSA study. Generalised linear mixed models (GLMMs) combine the properties of two statistical frameworks; linear mixed models,

incorporating random effects and repeated measures, which create inherent spatial and temporal correlation between observations, and generalised linear models outlined above (Bolker et al., 2009; Zuur et al., 2013). An assumption of the study was that provision of a more 'natural' summer low flow to rivers that had previously experienced high abstraction levels should result in a positive impact on the abundance and over-summer survival of 0+ and 1+ salmonid fishes (Environment Agency, 2009), thereby providing evidence for a direct benefit of flow restoration for salmonids in upland rivers in the UK.

METHODS

Study sites

Summer flow restoration was conducted on the Rivers Brennand and Whitendale (**Figure 1**). Both rivers rise in the fells of the Forest of Bowland in north Lancashire, UK. The Forest of Bowland is a designated Area of Outstanding Natural Beauty (AONB) and the upper catchments form the Bowland Fells SSSI. The rivers flow south to Footholme, giving rise to the River Dunsop, a tributary of the River Hodder, itself a tributary of the River Ribble. The River Ribble flows westward through the industrial city of Preston and enters the Irish Sea. The Hodder and its tributaries are part of a salmonid fishery designated under the Freshwater Fish Directive (78/659/EEC), which places statutory duties upon the EA to protect and enhance the fish populations within the fishery.

Water abstraction changes in the study area

Water is abstracted for public supply from both the Brennand and Whitendale at intake weirs in their uppermost reaches. Abstraction in the summer months, when demand for water is at a peak and effective rainfall at its lowest, formerly resulted in reduced flow downstream of the intakes. Approximately 3.5 km of each river was characterised by severely reduced flows during summer (Environment Agency, 2009). The quantity and quality of salmonid spawning substrate and juvenile habitat was also believed to be negatively affected by the water abstraction intakes on both rivers, contributing to an overall deterioration in salmonid habitat in the wider River Hodder catchment (Environment Agency, 2009).

In an attempt to limit abstraction from the Brennand and Whitendale, as part of the RSA programme, modifications were made to the public water supply abstraction licence to reduce maximum daily abstraction rates from April 2013. To accomplish this change the abstraction intake weirs on the Brennand and Whitendale were redesigned, with engineering work carried out during summer 2012. The intake aperture of each weir was rebuilt and a 2 mm fish screen fitted to prevent downstream fish entrainment. The most important modifications for downstream river flow was the addition of a 770 x 150 mm slot on each weir to allow flows to continue downstream during periods of low flow. The slots were installed to ensure abstraction could not occur when flows immediately below the intake weirs fell below 5.4 and 6.2 million litres per day (MLD) (0.062 and 0.74 m^3 s^{-1}) in the Brennand and Whitendale respectively. These river flows were chosen as the estimated natural summer flows that would be exceeded for 95% of the time (Qn95) at the points of the intakes (Environment Agency, 2009). The Environment Agency also undertook hydrological modelling to transpose the changes in

abstraction and river flow into average changes in juvenile salmonid habitat (wetted width) at the flow restored rivers. Estimated increases in wetted width were 36% for the River Brennand and 31% for the River Whitendale (Environment Agency, 2009).

Study design

In addition to the Brennand and Whitendale, where summer flows were restored (hereafter referred to as 'restored' rivers), an additional two control rivers, the Rivers Hareden and Langden were included in the study ('control' rivers). These rivers were selected for their proximity to the restored rivers (**Figure 1**) and because they had similar underlying geology, land use, flow magnitude and fish population composition (Environment Agency, 2010). Both control rivers had abstraction intakes with fish passes located on their lower reaches, but flows and sediment movement in the reaches above the intake weirs were assumed to approximate to a 'natural' situation. The upper reaches of the Brennand and Whitendale were unsuitable as controls as the intakes were so far up river that suitable habitat for salmonids was limited and intakes had no fish passes, confounding the effects of upstream to downstream differences. Thus the most appropriate approach was to identify adjacent rivers that were similar to the restored rivers, but without having abstraction intakes in the upper reaches.

Pre- and post- flow-restoration fish surveys were conducted at a total of 69 fish survey sites across restored and control rivers; Brennand (restored) 18 sites, Whitendale (restored) 17, Hareden (control) 19, Langden (control) 15, giving an approximately balanced design. Surveys were conducted solely in riffles to target juvenile salmonids within their preferred habitat and to minimise additional variation caused by differences in habitat type. Obvious overhanging banks, woody debris and braided areas were

avoided during site selection. This sampling strategy provided the best chance of attributing any changes in over-summer juvenile abundance to flow restoration (Environment Agency, 2011). Fish surveys were conducted at the restored rivers and control rivers each summer (July) and autumn (October) from 2011 to 2014. The interval between seasonal surveys, when temperatures were at their highest and rainfall lowest, was chosen to maximise the chance of detecting the effects of restored flow on the over-summer survival of 0+ and 1+ salmonids.

Each sampled site was 20 m in length and isolated with stop nets. Measurements of river-wetted width were taken at the top, middle and bottom of each survey site and these were used to derive an estimate of total site area surveyed. The entire site was fished in a single run using an Efish electric fishing backpack optimised for small individuals. To ensure sampling consistency, surveys were performed on the same or similar date in each year with the same equipment and a survey team comprising three people each with a defined role. Captured fish were identified to species with age class assigned in the field based on Fork Length (measured from the tip of the snout to the tip of the central caudal fin ray). Heavy rainfall, with associated turbid river flow that prohibited efficient fish capture, meant that only 6 sites were surveyed on the Hareden (control) in autumn 2013, and only 8 sites on the Langden (control) and only 2 sites on the Hareden in autumn 2014.

Data treatment and statistical models

Data exploration was undertaken following the protocol of Zuur et al. (2010) to examine the data for outliers in the response and explanatory variables, homogeneity and zero inflation in the response variable, collinearity between explanatory variables

and the nature of relationships between the response and explanatory variables. The only potential concern was a reduction in data for the River Hareden (control) in Autumn 2013 and 2014 and the River Langden (control) in Autumn 2014 due to severe weather, which resulted in some imbalance in the data for those years.

Data for *S. salar* and *S. trutta* were pooled for analysis. The habitat requirements of both species are similar, particularly at the juvenile stage (Armstrong et al., 2003), and the overall goal of the river flow restoration measures was to enhance salmonid populations. Consequently pooled data were used, with the assumption that model outcomes were comparable for both species.

GLMMs were fitted with counts of each juvenile age class (0+ and 1+) from autumn surveys as the response variable in each model. Assessment of residuals from an initial analysis applying a Poisson GLMM indicated overdispersion, most likely caused by high variance in the count response variable, which is common with count data (O'Hara and Kotze, 2010; Zuur et al., 2013). Consequently, for each juvenile age class the following negative binomial GLMM was fitted:

$$Count_{hijk} \sim NegBin(\mu_{hijk}, \theta)$$

$$E[Count_{hijk}] = \mu_{hijk}$$

$$\text{var}(Count_{hijk}) = \mu_{hijk} + (\mu_{hijk}^2 / \theta)$$

(θ = dispersion parameter for highly variable data, such as counts)

$Count_{hijk}$ = the kth autumn count of salmonids from period h in river i at site j

where: $Summer_{hij}$ = summer salmonid count from period h in river i at site j

period $h = 1 \ldots 2$

river $i = 1…4$

site $j = 1…69$

count $k = 1…220$

$$\eta_{hijk} \sim \beta_1 + \beta_2 \text{ x } Summer_{hij} + \beta_3 \text{ x } Period_h + \beta_4 \text{ x } River_i + \beta_5 \text{ x } Period_h \text{ x } River_i$$

$$a_j = N(0, \sigma^2)$$

$$b_j * Summer_{hij} = N(0, \sigma^2)$$

where η_{hijk} contains main terms (Summer, Period, River) and one interaction term (Period x River). Terms a_j and b_j are the random intercept (site) and random slope (summer count).

Period = 2 level factor (Before and After flow restoration)

River = 4 level factor (Brennand, Whitendale, Langden, Hareden)

Models were fitted to the following response variables:

1. Abundance of autumn 0+ salmonids (*S. salar* and *S. trutta*)
2. Abundance of autumn 1+ salmonids (*S. salar* and *S. trutta*)

For autumn salmonid abundance, autumn survey counts of both 0+ and 1+ were used as a measure of over-summer survival for each age class. The number of fish encountered at each survey site during autumn sampling was predicted to be a function of summer sampling counts at those same survey sites. Exploratory data plots confirmed that the relationship between summer and autumn survey counts was similar

for each river on average but that within these data there was considerable site-by-site variation in the relationship. I elected, *a priori*, to incorporate a fixed effect term for summer counts and a survey site random effect for summer count, as confirmed by my data exploration. A random intercept and slope model permits both survey-site level random effects for summer counts and inherent temporal and spatial correlation at the survey site level.

Model parameters were estimated in a Bayesian framework using the *R2jags* package (Su and Yajima, 2012) in the R statistical environment (R Development Core Team, 2016). Three independent Markov chains were run simultaneously. A burn-in of 10,000, thinning rate of 10 and 40,000 iterations were used, which resulted in 6,000 Markov Chain samples for each estimated parameter. Mixing (stationarity) and autocorrelation of chains were checked visually using trace plots and the Gelman-Rubin statistic (Brooks and Gelman, 1998). Autocorrelation was low and convergence was achieved in each case. Model validation showed no evidence of overdispersion, heterogeneity or non-linear patterns in the model residuals (Zuur et al., 2013). Spatial correlation was assessed with the use of variograms that estimate and plot the semi-variance of model residuals against spatial coordinates (see Zuur et al., 2009, 2013 and 2014 for details) and showed that any residual spatial correlation was likely to be weak. Variograms for the 0+ model are provided in **figures 12 to 15**, variograms for the 1+ model were similar and are not shown for brevity. The models were also used to simulate 'new' data using the appropriate distribution as part of the model-fitting process (Zuur et al., 2013; see **Chapter 3** for full consideration). Probability values for all models indicated that a negative binomial model was appropriate for the analysis of count data.

To investigate the effect of flow restoration on autumn abundance, model parameters were used to estimate the posterior mean count of 0+ and 1+ salmonids for each river and period with Bayesian 95% credible intervals. Given that the study aims were to investigate evidence that the change in flow in restored rivers would have a positive effect on the over-summer survival of juvenile salmonids, measured by autumn counts, and not to investigate any between river or period difference in the summer and autumn count relationship *per se*. In order to examine whether rivers differed importantly in their autumn fish abundance within each period, I estimated the posterior mean difference in autumn counts between rivers for each period whilst holding the summer counts term constant. To investigate if each river had experienced an important change in autumn abundance due to the flow change, the mean change in autumn counts between periods for each river were estimated. An additional goal was to determine if there was an important difference in the change in autumn salmonid abundance due to flow changes. To address this question the mean difference of the change in autumn counts between rivers was estimated.

The goodness of fit for each model was assessed using an 'out of sample' prediction method (see **Chapters 3 & 4** for details). Graphical results of this method are given in **figures 16 and 17**. Both the 0+ model and 1+ model had 44% of observed data points within the estimated posterior mean distributions.

RESULTS

Data summary

A total of 37,972 juvenile (0+ and 1+) salmonids were caught over the 2011 to 2014 period. The catch of 0+ and 1+ *S. salar* and *S. trutta* from surveys from each river and

in each year are summarised in **Tables 1a-d**. *S. salar* represented 30.6% of the total salmonid catch with the remainder *S. trutta*. A clear difference in the catch of *S. salar* is seen for the control Rivers Hareden and Langden. No *S. salar* were caught in the River Hareden, and the River Langden contributed just 1.3% of the total catch of *S. salar* from all the rivers surveyed between 2011 and 2014.

Model results

0+ salmonids

An important increase was observed in the posterior mean count of autumn 0+ salmonids at both restored rivers after flow restoration (**Figure 2**). The posterior mean count per site of autumn 0+ salmonids in the Brennand (**Table 2**) increased considerably by 53.8% from 41.2 to 63.4. The River Whitendale showed a smaller increase of 18.3% in posterior mean count per site (**Table 2** and **Figure 2**) from 50.7 in the before restoration period to 60.0 in the after restoration period. The posterior mean count of autumn 0+ salmonids at both control rivers showed the largest increases (**Table 2** and **Figure 2**). The posterior mean count on the River Langden increased substantially by 104.3% from 32.7 in the before period to 66.8 in the after period. The posterior mean count on the River Hareden also increased substantially by 109.2% from 33.6 in the before restoration period to 70.3 in the after period.

The before – after change in posterior mean count per site for the River Brennand was 22.2 (**Table 3**) and was important with the lower 95% credible interval clearly greater than zero (**Figure 3**). The before – after change in posterior mean count per site for the River Whitendale was 9.3 (**Table 3**) and this was also important although the lower 95% credible interval (0.28) is close to zero (**Table 3** and **Figure 3**)

implying that the change for the Whitendale was not as important as for the Brennand. The before – after change in posterior mean count per site for the River Langden was 34.0 and for the River Hareden was 36.7 (**Table 3**). Changes in posterior mean count per site at both control rivers were important and clearly greater than the changes at the restored rivers (**Figure 3**).

Estimates of the differences in the before – after change in posterior mean count per site between rivers showed the River Brennand had a clearly greater before – after change than the Whitendale, 12.9 (**Table 4** and **Figure 4**). The before – after change in posterior mean count per site for the River Brennand was lower than both controls (**Table 4** and **Figure 4**), with a lower posterior mean change than the River Langden of -11.8 and a lower posterior mean change than the River Hareden of -14.5. The presence of zero in the tails of the credible intervals suggests that these differences are not important and implies that over-summer survival of salmonids in the River Brennand changed in a similar way to that of the controls. The control rivers showed no difference in the before – after change in posterior mean count per site (**Table 4** and **Figure 4**), suggesting that changes in over-summer survival over the study period were close to identical in the control rivers. The before – after change for the River Whitendale was clearly less than either of the control rivers (**Table 4** and **Figure 4).** The posterior mean difference in change between the Whitendale and the River Langden was -24.7 and between the Whitendale and the River Hareden was -27.4 with no zeros in the credible intervals. This result suggests that the change in over-summer survival of 0+ salmonids in the River Whitendale was claerly less than the controls and marginally less than the River Brennand over the study period.

The posterior mean count per site of autumn 0+ for the River Brennand in the period before flow restoration (**Table 5** and **Figure 5**) was lower than the Whitendale by 9.6, zero in the credible intervals imply no important difference in mean count per site between these rivers (**Figure 5**). This result suggests that over-summer survival in these two rivers was broadly similar in the two years prior to flow restoration. Compared with the control rivers in the before period, the posterior mean count per site of autumn 0+ salmonids for the River Brennand was greater than the River Langden by 8.4 and the River Hareden by 7.5, but not important. The presence of zero in the tails of the lower credible intervals suggests broadly similar over-summer survival in the Brennand and control rivers (**Figure 5**) in the two years prior to flow restoration. The difference in posterior mean count per site of autumn 0+ salmonids for the control rivers in the before restoration period (**Table 5**) was -0.9, indicating no important difference between the two control rivers (**Figure 5**) and suggesting that over-summer survival was near identical in these rivers in the two years prior to flow restoration. The posterior mean count per site of autumn 0+ salmonids for the River Whitendale was clearly greater than that of the control rivers with no zero in the credible intervals (**Table 5** and **Figure 5**). Posterior mean count per site were greater than for the Langden by 18.0 and greater than the Hareden by 17.0, suggesting that over-summer survival was clearly greater in the River Whitendale in the two years prior to flow restoration. Overall the results for the before flow restoration period suggest that the over-summer survival of 0+ salmonids in the rivers requiring flow restoration was at worse no different to the control rivers and in one case, the River Whitendale, was clearly better than the controls. When the difference in posterior mean count per site of autumn 0+ salmonids was compared between rivers in the after flow restoration period, there were no

important differences (**Table 6** and **Figure 6**), implying broadly similar over-summer survival across all study rivers in the two year period after flow restoration.

1+ salmonids

Clear increases were observed in the posterior mean count per site of autumn 1+ salmonids for the restored rivers Brennand and Whitendale in the two-year period following flow restoration (**Figure 7**). The posterior mean count per site of autumn 1+ salmonids in the Whitendale (**Table 7**) increased by 39.5% from 20.5 to 28.6 and from 18.2 to 23.0 in the River Brennand, an increase of 26.4% (**Table 7** and **Figure 7**). The posterior mean count per site of autumn 1+ salmonids at the control rivers showed different increases (**Table 7** and **Figure 7**). The posterior mean count on the River Langden increased from 20.5 in the before restoration period to 23.5 in the after period, a 14.6% increase. The posterior mean count for the River Hareden increased by 47.8% from 20.3 in the before period to 30.0 in the after restoration period.

The before – after change in posterior mean count per site for the River Brennand was 4.8 and important with no zero in the 95% credible intervals (**Table 8** and **Figure 8**). The before – after change in posterior mean count for the River Whitendale was 8.1 and also important. The before – after change in posterior mean count for the River Langden was 3.0 and not important with zero in the lower credible interval, suggesting no before – after change in posterior mean count per site over the two year after restoration period. The before – after change in posterior mean count for the River Hareden was 9.7 and important with no zero in the credible intervals. These results indicate that both restored rivers showed clear increases in over-summer survival in the two-year period following flow restoration. However, estimates of the differences

in the before – after change in posterior mean count per site for 1+ salmonids revealed no clear differences (**Table 9** and **Figure 9**). This result shows that the before – after restoration changes in over-summer survival of 1+ salmonids were similar across restored and control rivers.

There was no important difference in the posterior mean count of 1+ salmonids across all rivers in the before-restoration period (**Table 10** and **Figure 10**), indicating that over-summer survival of 1+ salmonids was similar in all rivers in the two years prior to flow restoration. In the after-restoration period (**Table 11** and **Figure 11**) the River Brennand had a slightly lower posterior mean count per site of 1+ autumn salmonids than the River Whitendale, but zero in the credible interval indicates that this result is not important. Hence, over-summer survival in the restored rivers was broadly similar in the two-year period after flow restoration. The River Brennand showed a lower posterior mean count per site than the River Hareden of -7.1, but this is not important. The posterior mean count per site for the River Brennand was broadly similar to that for the River Langden, with a posterior mean difference of just -0.5. The River Whitendale had a higher posterior mean count per site of 1+ salmonids than the River Langden in the after restoration period, though this is not important due to zero in the credible intervals. The River Whitendale had a similar posterior mean count of 1+ salmonids to the River Hareden in the after restoration period, with a posterior mean difference of -1.4. The River Langden had a lower posterior mean count of 1+ salmonids than the River Hareden of -6.6 but this was not important. Thus, despite some subtle patterns the results suggest that the general pattern in over-summer survival of 1+ salmonids was broadly similar across the study rivers during the study period.

DISCUSSION

The goal of the present study was to assess the short-term effectiveness of flow restoration measures on the over-summer survival of juvenile salmonids in two upland rivers in the UK. Four rivers were surveyed in a Before-After-Control-Impact (BACI) design, with two rivers undergoing flow restoration and two acting as control rivers. In my mixed effects models, the autumn 0+ salmonid count is the response variable and the summer 0+ count is used as an explanatory variable in the fixed part of the model. Additionally, summer 0+ count is used as a random effect for each survey site in each river to allow for random between-site variations in summer 0+ counts. Within this analytical framework the response variable provided a measure of over-summer survival. The evidence demonstrating short-term benefits of flow restoration was limited. Broadly, my models suggest that over the four-year monitoring period, the over-summer survival of juvenile salmonids in the Rivers Brennand and Whitendale was enhanced, but not clearly when compared with the control rivers Langden and Hareden over the same period. Within the broad results there are notable river and age-class specific differences in changes over the study period.

Some of my findings suggest that flow restoration may have provided a short-term benefit to 0+ salmonids in the River Brennand and the River Whitendale (**Figures 2** and **3**). The magnitude of change in the over-summer survival of 0+ salmonids in the River Brennand was clearly greater than in the River Whitendale, but less than in the control rivers, though the latter difference was not important (**Figure 4**). This finding implies that while the changes in over-summer survival of 0+ salmonids in the River Brennand were greater then in the River Whitendale, they are at best no different to the controls, implying no clear short-term benefit of flow restoration when compared with

controls. When the magnitude of change observed in the River Whitendale was compared with that of the controls (**Figure 4**) it was clearly less, implying that over-summer survival of 0+ salmonids in the River Whitendale was not improved in the short-term when compared with that in the control rivers over the same period.

The short-term pattern in over-summer survival of 0+ salmonids in the River Whitendale was notable, and clearly different to the other study rivers. When the posterior mean count per site of autumn 0+ salmonids for the River Whitendale was compared with that for the controls before flow restoration (**Figure 5**), it was clearly greater. This finding suggests that, although the Whitendale was considered as requiring flow restoration, the two years of pre-flow restoration data do not provide empirical support for this opinion. Indeed, over-summer survival of 0+ salmonids in the River Whitendale was considerably higher than that of any of the controls in the two-year period prior to flow restoration. When the posterior mean count per site of autumn 0+ salmonids for the River Brennand was compared with that for the controls in the before flow restoration period (**Figure 5**) it also appeared greater but the difference was not important. This finding suggests that over-summer survival in the River Brennand was broadly similar to the control rivers in the before period. Again, this evidence does not appear to support the view that the River Brennand required low flow restoration, an expectation would be that over-summer survival in the River Brennand was lower than that for the controls in the before period. One of the chief goals of implementing flow restoration in the present study was to enhance over-summer survival of juvenile salmonids in response to reduced summer flows linked to the water company abstraction activity, and the assumed risk to juvenile salmonids from low summer flows was a key factor in the case made to alter the water company abstraction licences

(Environment Agency, 2009). The decision to implement flow restoration was supported by a limited amount of routine fish monitoring data, however these data were not collected with a view to considering over-summer survival, which was the case in the current study (Environment Agency, 2009).

My results provide modest evidence that low flow restoration afforded short-term benefits to the over-summer survival of 1+ salmonids in both the River Whitendale and Brennand (**Tables 7** and **8, Figures 7** and **8**). When differences in the before – after changes in 1+ salmonids are estimated between rivers, the pattern is less marked and there was no clear difference between restored and control rivers (**Figure 9**). The absence of a strong effect is further supported by the counts of 1+ fish between rivers in both the before restoration period (**Figure 10**) and following restoration works (**Figure 11**), which do not show an important difference in either period. The models suggest that the restored rivers and the control rivers had similar counts of autumn 1+ salmonids in both the before and after restoration periods. This finding implies that over-summer survival for this age class is similar across all study rivers over the study period.

My overall results are partly consistent with those from a study of restored flows in Bridge River, British Columbia, Canada (Bradford et al., 2011). Their 13-year monitoring programme failed to show clear benefits for juvenile salmonids in reaches where flows were enhanced by greater dam releases, although considerable benefits were found in reaches that were previously completely dewatered but then re-wetted by the new releases. Their overall conclusion was that results did not support a simplistic notion of 'more water equals more fish' and that ecological responses to changes in flow regime may not be readily predicted owing to factors other than flow (Lancaster and Downes, 2010; Poff and Zimmerman, 2010). A key factor determining juvenile

salmonid survival and growth are negative density-dependent effects, (Crisp, 1993; Elliott, 1995), which may swamp effects such as enhanced river flows and make it difficult to detect positive changes. River flows are likely to be an important control for density dependence since flow is a major determinant of physical habitat structure (Bunn and Arthington, 2002) that in turn determines the competitive space for individuals. Density dependence and river flow can interact so that survival can be affected by density during lower mean flow years and have a significantly lesser effect at higher mean flows (Richard et al., 2013). This interaction provides an opportunity for river flow management to be used to ameliorate density dependence and instil some resilience in populations at risk of climatic or anthropogenic events that reduce river flows. Density-dependent effects may have operate in the Rivers Brennand and Whitendale and on-going monitoring to fully understand these effects will be required.

A potentially confounding effect in my study, and others like it, is that the major construction works may have had a short-term negative effect on juvenile salmonids. The intake weirs on the Rivers Brennand and Whitendale were altered during 2012 to restore summer low flow and these works could have had a detrimental effect on the salmonids within these rivers. Effects could have arisen through disturbance, increased sediment load, or the potential release of contaminants (Warren et al., 2015; **Chapter 1**). A possible outcome would be a limited or negative response to flow restoration when compared to the control rivers, at least in the two years of sampling immediately following the works. Thus, in the longer term the abundance and over-summer survival of juvenile salmonids in the restored rivers may increase to the same relative levels as the controls, or exceed them. A negative, short-term response is a common feature of many habitat restoration efforts. For example, dam removal frequently has short-term

negative ecological impacts on rivers, but with longer-term positive effects on flow heterogeneity and biotic diversity (Bednarek, 2001). Despite this, my analysis offers no evidence for a short-term negative effect, with no indication of decreases in the over-summer survival of 0+ and 1+ salmonids in response to construction work or other unmeasured factors. Whether longer-term positive effects of restoration will manifest themselves will require more than two years of post-restoration monitoring.

A potential criticism of the present study is in the choice of control rivers. Identification of appropriate controls for impact assessment studies in the natural environment is notoriously difficult, and identifying sampling units that truly represent 'controls' is a contentious subject (Underwood, 1991; Downes, 2010). It is generally agreed that the ideal control should be identical to the impact location in all aspects other than the impact under study. In reality this condition is rarely satisfied, and some pragmatic relaxing of control selection criteria is a practical necessity. In the present study, the control rivers were selected based on their geographical location, size, underlying geology and were known to support salmonid populations (Environment Agency, 2010).

My analysis showed that the pre-restoration abundance and over-summer survival of juvenile salmonids at the Rivers Brennand and Whitendale provided limited evidence that water abstraction was negatively impacting juvenile salmonids. Only two years of pre-restoration data were collected at the restored and control rivers, which began after the decision to restore summer flows had already been made. The total cost of delivering the flow restoration scheme for the rivers Brennand and Whitendale exceeded 5.3 million pounds sterling (Head of Water Resources, United Utilities, pers comm). The cost of carrying out the four years of fish surveys at control and impacted

rivers was approximately 2% of the total flow restoration scheme costs (Senior Environmental Monitoring Officer, Environment Agency, pers comm). Based on this proportion of expenditure, my recommendation for planned restoration works of this nature is for fuller investment in data collection several years prior to the design and implementation of costly restoration schemes to ensure the evidence to justify implementation of restoration works is robust. In the present case, a comparison of mean juvenile salmonid abundances across study rivers would have shown that abundances in the River Whitendale exceeded those of the other rivers in the two years prior to flow restoration, thereby challenging the assumptions about negative impacts on salmonids and the likely direction of benefits from flow restoration to be reconsidered. Investment in pre-scheme monitoring is important if river managers are to gain a fuller understanding of spatial and temporal variability in riverine biota. Even where data suggest remedial work is required, they can be used to set realistic levels of expectation in terms of the likely biological response to any measures put in place. This refinement is especially important where the feature of biological interest can exhibit high inter-annual variability and long-term trends, which is likely to be the case for salmonids (Poff et al., 1997; Armstrong et al., 2003; Warren et al., 2015). Additional analyses that examine biotic variables other than fish abundance could potentially be employed. Thus, growth rates may have been enhanced through flow restoration and the study design used here lends itself to providing the necessary data to fulfil an investigation of this sort (see **Chapter 6**).

A possible improvement to the study design would have been to stagger the timing of the flow restoration between rivers, for example restore one river in 2012 and the second river at least two years later and monitor for two years further, essentially a

six year study. This would have allowed a comparison to be made across each 2-year period (Before, After one river, After both rivers). The changes found in the first restored river could then be compared with the control rivers and the unrestored river to allow any potential benefits to be expressed in a more meaningful context; namely what happens if no restoration takes place. This would allow quantitative statements to be made on the scale of benefits compared with controls and also not having carried out restoration. Essentially, the study in its current design is confounded to a degree by temporal effects and lack of a treatment level 'requiring restoration but not restored'.

Application of Bayesian GLMMs in the current study proved robust in dealing with a relatively complex dataset, specifically in handling unbalanced nested data that showed an inherent lack of dependency due to repeated measures at sampling sites, and a highly varied non-normal response variable (fish survey counts). Such models display flexibility by allowing the estimation of a posterior distribution of differences between parameters and across levels of factors, such as before-and-after restoration and among rivers and sites. These are relatively straightforward procedures within a Bayesian framework, once a basic understanding of parameter estimation and model fitting is achieved. Such estimates in a frequentist framework are less straightforward, and often unattainable, since they are founded on the absurd concept of null hypotheses and theoretical re-running of experiments or data collection (Ellison, 1996; Zuur et al. 2013; Kruschke, 2015; **Chapter 2**). The novel nature of the present study meant that I used non-informative priors in my models. A potential refinement would be to define informative priors based on empirical evidence or expert judgement and contrast the predictions of models with non-informative and informative priors. The application of Bayesian GLMMs and similar models offer powerful analytical tools for ecological

studies and environmental impact assessments, especially where prior knowledge from other studies can be used. The adoption of Bayesian inference in this manner is highly recommended and should become the default for ecologists and environmental managers (Ellison, 1996).

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TABLES

Table 1a. Summary of 0+ and 1+ salmonids caught in electrofishing surveys split by river and year. r = restored river, c = control river.

		Year				
Species	River	2011	2012	2013	2014	Total
S. salar	Brennand (r)	1707	1038	1774	1881	6400
	Hareden (c)	0	0	0	0	0
	Langden (c)	130	58	88	207	483
	Whitendale (r)	1077	1052	1211	1391	4731
	Total	2914	2148	3073	3479	11614
S. trutta	Brennand (r)	1482	1578	1774	1570	6404
	Hareden (c)	1768	1856	1106	418	5148
	Langden (c)	1695	1628	2684	1876	7883
	Whitendale (r)	1465	1409	2174	1875	6923
	Total	6410	6471	7738	5739	26358
Total salmonids	Brennand (r)	3189	2616	3548	3451	12804
	Hareden (c)	1768	1856	1106	418	5148
	Langden (c)	1825	1686	2772	2083	8366
	Whitendale (r)	2542	2461	3385	3266	11654
	Total	9324	8619	10811	9218	37972

Table 1b. Summary of 0 + salmonids caught in electrofishing surveys split by river and year. r = restored river, c = control river.

		Year				
Species	River	2011	2012	2013	2014	Total
S. salar	Brennand (r)	1229	557	1144	1483	4413
	Hareden (c)	0	0	0	0	0
	Langden (c)	9	3	77	118	207
	Whitendale (r)	708	663	527	817	2715
	Total	1946	1223	1748	2418	7335
S. trutta	Brennand (r)	1115	1186	1267	975	4543
	Hareden (c)	720	1170	667	161	2718
	Langden (c)	927	1100	1757	1215	4999
	Whitendale (r)	1139	1061	1646	1153	4999
	Total	3901	4517	5337	3504	17259
Total salmonids	Brennand (r)	2344	1743	2411	2458	8956
	Hareden (c)	720	1170	667	161	2718
	Langden (c)	936	1103	1834	1333	5206
	Whitendale (r)	1847	1724	2173	1970	7714
	Total	5847	5740	7085	5922	24594

Table 1c. Summary of 1 + salmonids caught in electrofishing surveys split by river and year. r = restored river, c = control river.

		Year				
Species	River	2011	2012	2013	2014	Total
S. salar	Brennand (r)	478	481	630	398	1987
	Hareden (c)	0	0	0	0	0
	Langden (c)	121	55	11	89	276
	Whitendale (r)	369	389	684	574	2016
	Total	968	925	1325	1061	4729
S. trutta	Brennand (r)	367	392	507	595	1861
	Hareden (c)	1048	686	439	257	1924
	Langden (c)	768	528	927	661	2884
	Whitendale (r)	326	348	528	722	2430
	Total	2509	1954	2401	2235	9099
Total salmonids	Brennand (r)	845	873	1137	993	3848
	Hareden (c)	1048	686	439	257	2430
	Langden (c)	889	583	938	750	3160
	Whitendale (r)	695	737	1212	1296	3940
	Total	3477	2879	3726	3296	13378

Table 1d. Summary of proportion of 1+ to 0+ salmonids caught in electrofishing surveys split by river and year. r = restored river, c = control river. Proportions = 1+/0+

		Year				
Species	River	2011	2012	2013	2014	Total
S. salar	Brennand (r)	0.39	0.82	0.55	0.27	0.45
	Hareden (c)	NA	NA	NA	NA	NA
	Langden (c)	13.44	18.33	0.14	0.75	1.33
	Whitendale (r)	0.52	0.59	1.30	0.70	0.74
	Total	0.50	0.76	0.76	0.44	0.64
S. trutta	Brennand (r)	0.57	0.33	0.40	0.61	0.41
	Hareden (c)	1.46	0.59	0.66	1.60	0.71
	Langden (c)	0.83	0.48	0.53	0.54	0.58
	Whitendale (r)	0.29	0.33	0.32	0.63	0.49
	Total	0.64	0.43	0.45	0.64	0.53
Total salmonids	Brennand (r)	0.36	0.50	0.47	0.40	0.43
	Hareden (c)	1.46	0.59	0.66	1.60	0.89
	Langden (c)	0.95	0.53	0.51	0.56	0.61
	Whitendale (r)	0.38	0.43	0.56	0.66	0.51
	Total	0.59	0.50	0.52	0.56	0.54

Table 2. Posterior mean estimates of autumn 0+ counts for each river and period. CrI is the 95% Bayesian credible interval.

River	Period	Mean	2.5% quant.	97.5% quant.	% mean change
Brennand	Before	41.2	34.6	48.6	
	After	63.4	54.8	72.8	53.8
Whitendale	Before	50.7	43.3	58.9	
	After	60.0	51.6	69.5	18.3
Langden	Before	32.7	27.8	38.6	
	After	66.8	56.3	79.1	104.3
Hareden	Before	33.6	27.9	40.0	
	After	70.3	52.9	91.5	109.2

Table 3. Posterior mean estimates of the before-after change in 0+ counts for each river. CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold.

River	Posterior mean	Lower CrI	Upper CrI
Brennand	22.2	**13.7**	**31.3**
Whitendale	9.3	**0.28**	**19.0**
Langden	34.0	**22.7**	**46.6**
Hareden	36.7	**19.7**	**58.2**

Table 4. Posterior mean estimates of differences in before-after changes of 0+ counts between rivers. CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold. Differences between each river: BW = Brennand - Whitendale, BL = Brennand - Langden, BH = Brennand - Hareden, WL = Whitendale - Langden, WH = Whitendale - Hareden, LH = Langden - Hareden.

River contrasts	Posterior mean	Lower CrI	Upper CrI
BW	12.9	**0.3**	**26.0**
BL	-11.8	-27.2	2.2
BH	-14.5	-37.4	4.6
WL	-24.7	**-40.5**	**-9.9**
WH	-27.4	**-50.3**	**-8.3**
LH	-2.7	-27	17.7

Table 5. Posterior mean estimates of differences in 0+ counts between rivers for the before restoration period. CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold. Differences between each river: BW = Brennand and Whitendale, BL = Brennand and Langden, BH = Brennand and Hareden, WL = Whitendale and Langden, WH = Whitendale and Hareden, LH = Langden and Hareden.

River contrasts	Posterior mean	Lower CrI	Upper CrI
BW	-9.6	-19.9	0.9
BL	8.4	-0.5	17.2
BH	7.5	-1.1	16.6
WL	18.0	**8.6**	**27.6**
WH	17.0	**7.7**	**27.1**
LH	-0.9	-8.9	7.2

Table 6. Posterior mean estimates of differences in autumn 0+ counts between rivers for the after restoration period. CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold. Differences between each river: BW = Brennand - Whitendale, BL = Brennand - Langden, BH = Brennand - Hareden, WL = Whitendale - Langden, WH = Whitendale - Hareden, LH = Langden - Hareden.

River contrasts	Posterior mean	Lower CrI	Upper CrI
BW	3.3	-9.3	16.0
BL	-3.4	-18.2	10.3
BH	-7.0	-29.2	12.9
WL	-6.7	-21.7	7.1
WH	-10.3	-33.0	9.1
LH	-3.6	-27.4	16.8

Table 7. Posterior mean estimates of autumn 1+ counts for each river and period. CrI is the 95% Bayesian credible interval.

River	Period	Posterior mean	Lower CrI	Upper CrI	% mean change
Brennand	Before	18.2	15.4	21.4	
	After	23.0	19.7	26.5	26.4
Whitendale	Before	20.5	17.3	24.1	
	After	28.6	24.3	33.5	39.5
Langden	Before	20.5	17.4	24.1	
	After	23.5	19.4	28.2	14.6
Hareden	Before	20.3	17.4	23.5	
	After	30.0	22.2	40.0	47.8

Table 8. Posterior mean estimates of the before-after change in 1+ counts for each river. CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold.

River	Posterior mean	Lower CrI	Upper CrI
Brennand	4.8	**1.1**	**8.6**
Whitendale	8.1	**3.3**	**13.1**
Langden	3.0	-1.8	8.0
Hareden	9.7	**1.6**	**19.7**

Table 9. Posterior mean estimates of differences in before-after changes of 0+ counts between rivers. CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold. Differences between each river: BW = Brennand - Whitendale, BL = Brennand - Langden, BH = Brennand - Hareden, WL = Whitendale - Langden, WH = Whitendale - Hareden, LH = Langden - Hareden.

River contrasts	Posterior mean	Lower CrI	Upper CrI
BW	-3.4	-9.7	2.9
BL	1.8	-4.5	7.9
BH	-5.0	-15.6	4.3
WL	5.2	-1.8	12.0
WH	-1.6	-12.5	7.8
LH	-6.8	-17.8	2.8

Table 10. Posterior mean estimates of differences in 1+ counts between rivers for the before period. CrI is the 95% Bayesian credible interval. Credible intervals that do not contain zero in bold. Differences between each river: BW = Brennand and Whitendale, BL = Brennand and Langden, BH = Brennand and Hareden, WL = Whitendale and Langden, WH = Whitendale and Hareden, LH = Langden and Hareden.

River contrasts	Posterior mean	Lower CrI	Upper CrI
BW	-2.3	-6.8	2.3
BL	-2.3	-6.9	2.2
BH	-2.1	-6.2	2.2
WL	0.0	-4.8	4.8
WH	0.2	-4.4	4.8
LH	0.2	-4.2	4.8

Table 11. Posterior mean estimates of differences in 0+ counts between rivers for the after period. CrI is the 95% Bayesian credible interval. Differences between each river: BW = Brennand - Whitendale, BL = Brennand - Langden, BH = Brennand - Hareden, WL = Whitendale - Langden, WH = Whitendale - Hareden, LH = Langden - Hareden.

River contrasts	Posterior mean	Lower CrI	Upper CrI
BW	-5.7	-11.7	0.4
BL	-0.5	-6.1	5.0
BH	-7.1	-17.6	1.6
WL	5.2	-1.1	11.4
WH	-1.4	-12.2	7.8
LH	-6.6	-17.1	2.4

FIGURES

Figure 1. Location of study rivers. Flow restored rivers in top-right of panel, River Brennand on left, River Whitendale on right (Red circles show fish survey sites). Control rivers in bottom-left of panel, River Langden on left, River Hareden on right (Red circles show fish survey sites).

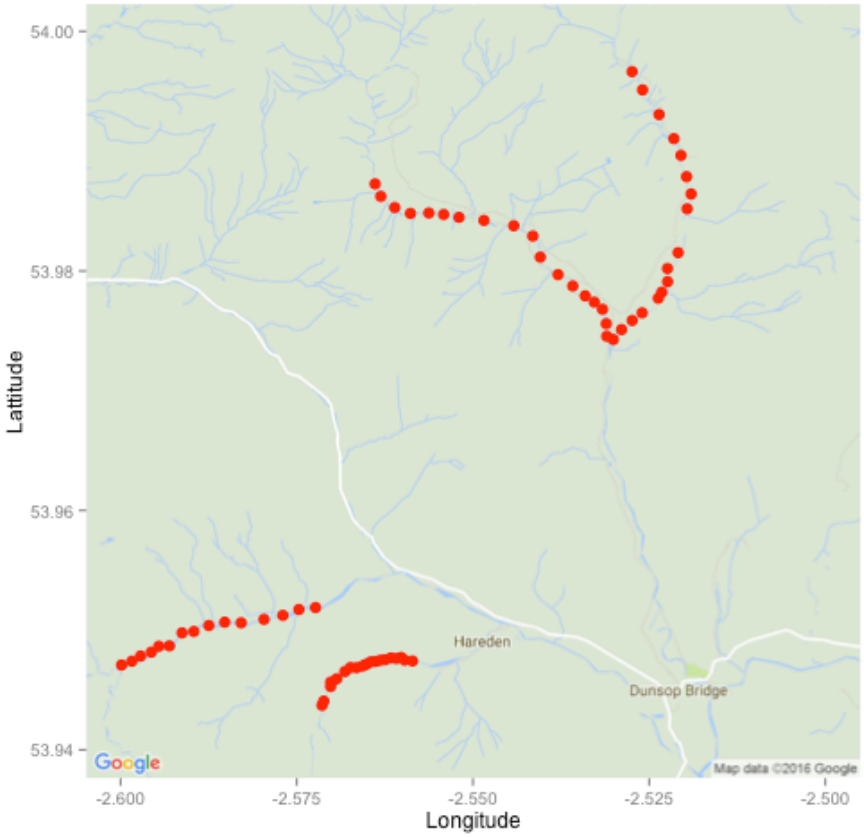


Figure 2. Posterior mean count per site of autumn 0+ salmonids for each period (B = before restoration, After = after restoration) in each river (B = Brennand; W = Whitendale; L = Langden, H = Hareden). Vertical lines are 95% Bayesian credible intervals. Open circles are control rivers, closed circles are flow-restored rivers. Dashed lines aid visualisation of change in counts between periods.

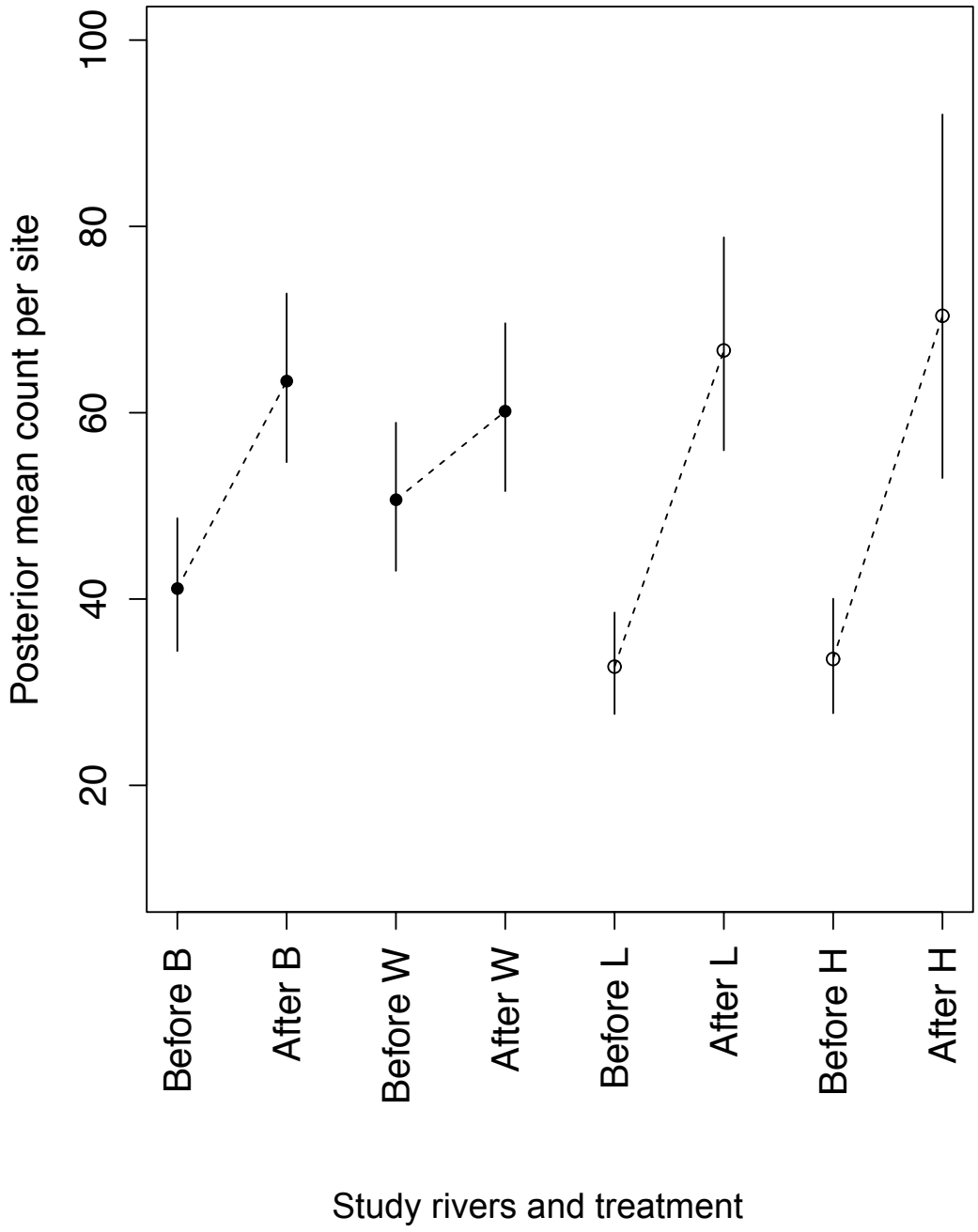


Figure 3. Posterior mean estimates of the before-after change in mean count per site of autumn 0+ salmonids for each river. Vertical lines are 95% Bayesian credible intervals. Open circles are control rivers, closed circles are flow restored rivers. Horizontal line at zero indicates no change.

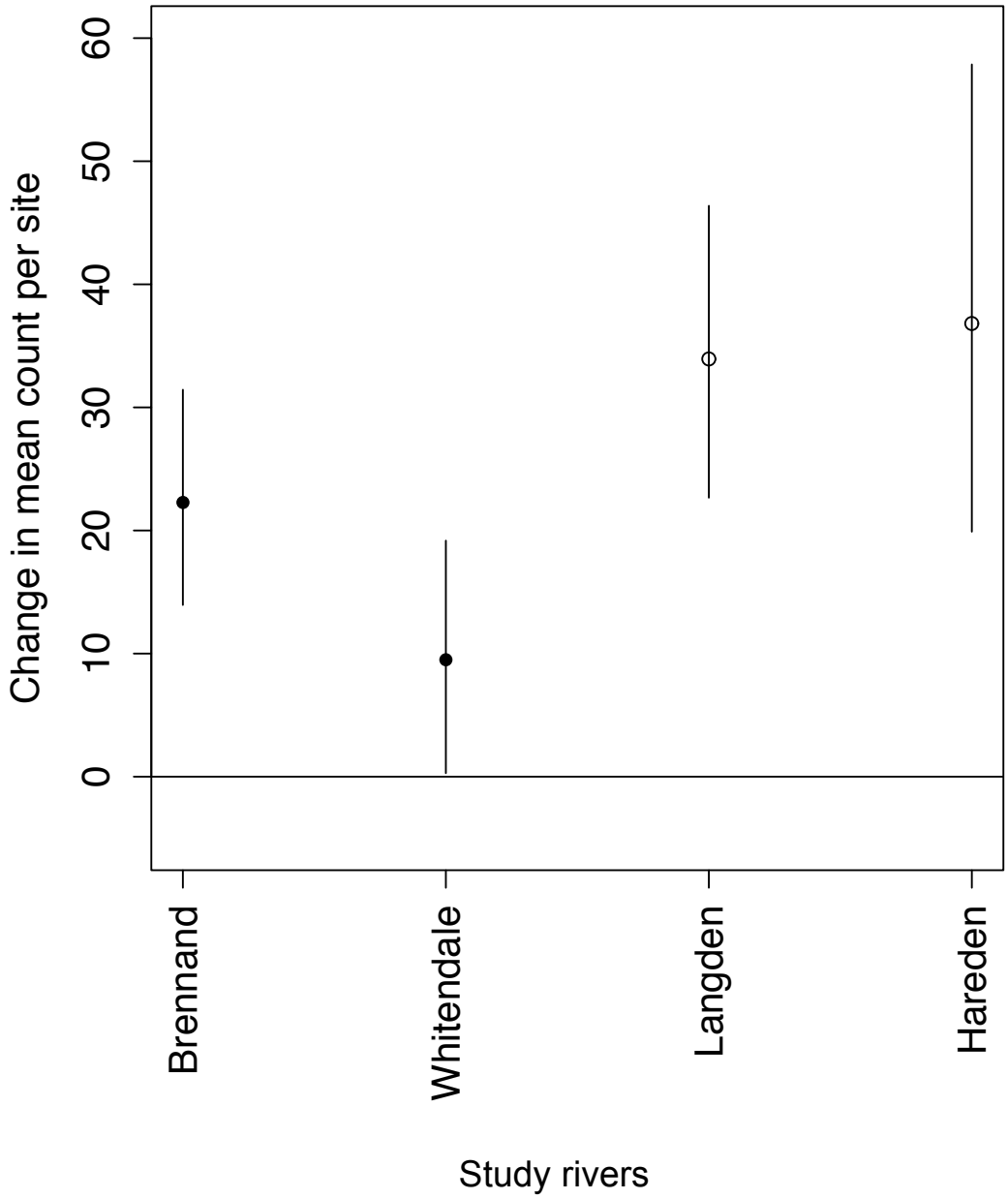


Figure 4. Posterior mean estimates of the differences in the before-after changes in mean count per site of autumn 0+ salmonids between rivers. Vertical lines are 95% Bayesian credible intervals. Horizontal line at zero difference in change. Differences between each river: BW = Brennand and Whitendale, BL = Brennand and Langden, BH = Brennand and Hareden, WL = Whitendale and Langden, WH = Whitendale and Hareden, LH = Langden and Hareden.

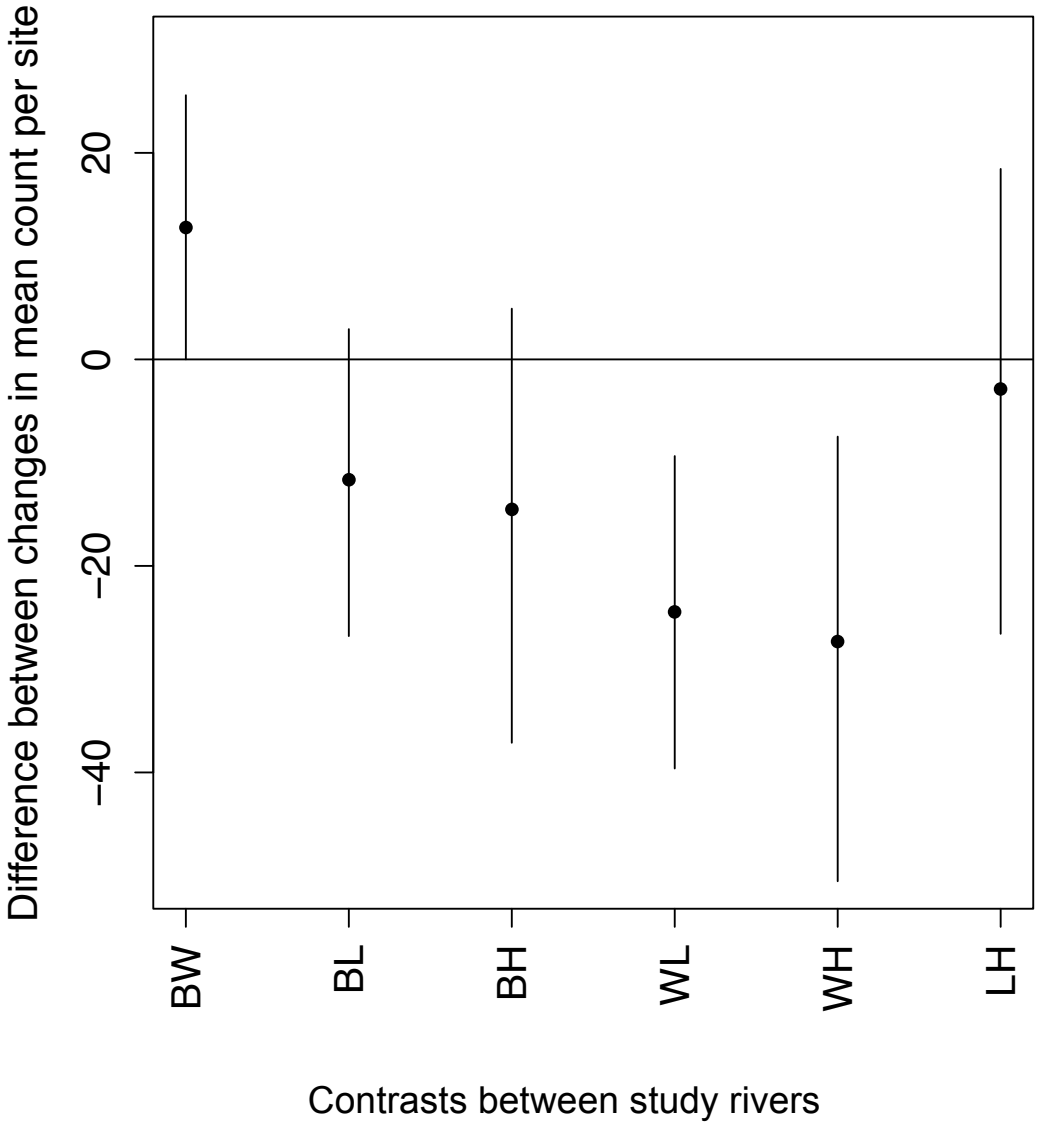


Figure 5. Posterior mean estimates of differences in mean count per site of autumn 0+ salmonids between rivers for the before period Vertical lines are 95% Bayesian credible intervals. Horizontal line at zero change. Differences between each river: BW = Brennand and Whitendale, BL = Brennand and Langden, BH = Brennand and Hareden, WL = Whitendale and Langden, WH = Whitendale and Hareden, LH = Langden and Hareden.

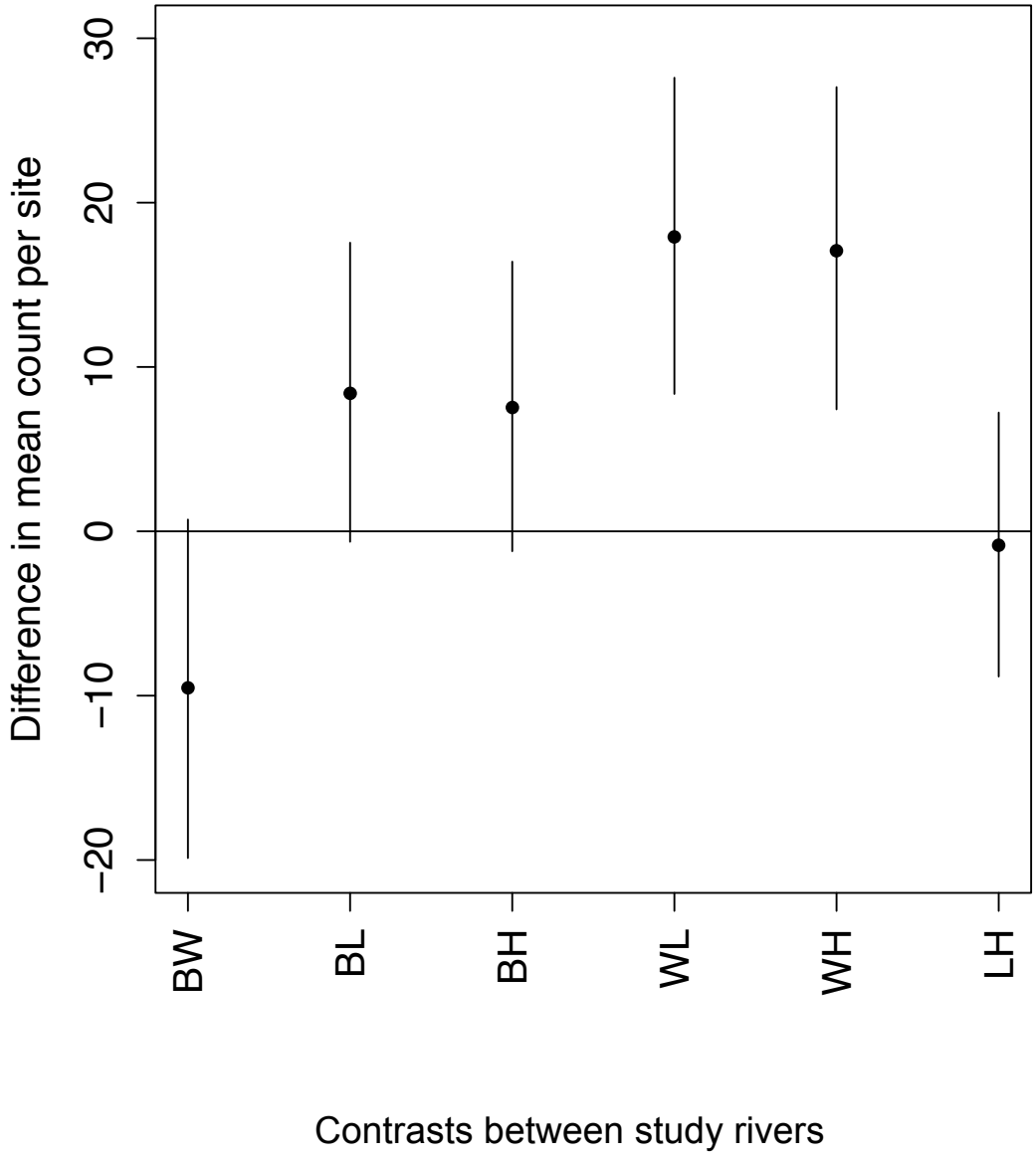


Figure 6. Posterior mean estimates of differences in mean count per site of autumn 0+ salmonids between rivers for the after period. Vertical lines are 95% Bayesian credible intervals. Horizontal line at zero change. Differences between each river: BW = Brennand and Whitendale, BL = Brennand and Langden, BH = Brennand and Hareden, WL = Whitendale and Langden, WH = Whitendale and Hareden, LH = Langden and Hareden.

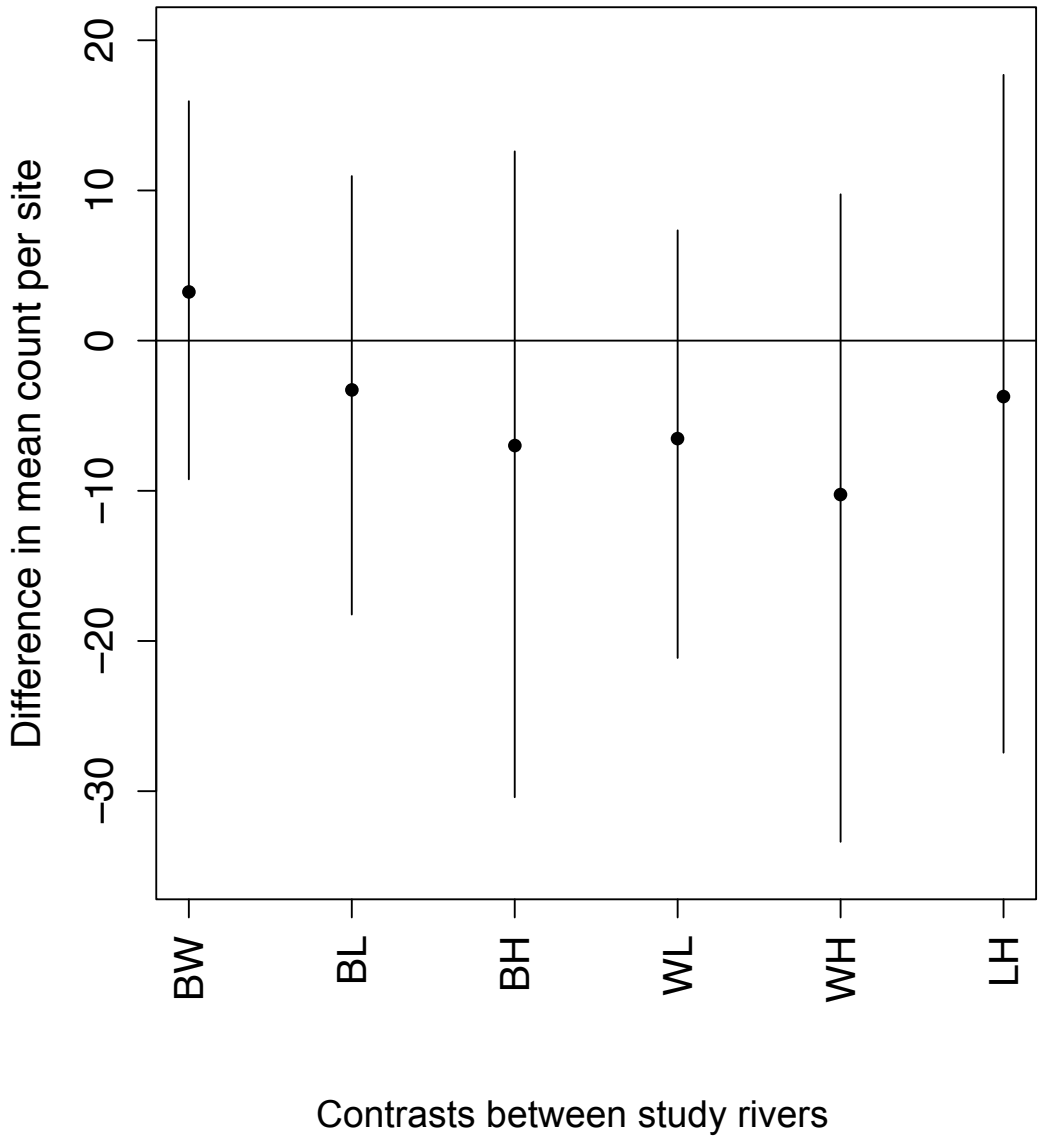


Figure 7. Posterior mean count per site and 95% credible intervals of autumn 1+ salmonids in each river and period. Vertical lines = 95% Bayesian credible intervals. Open circles are control rivers, closed circles are flow-restored rivers. Dashed lines aid visualisation of change in counts between periods.

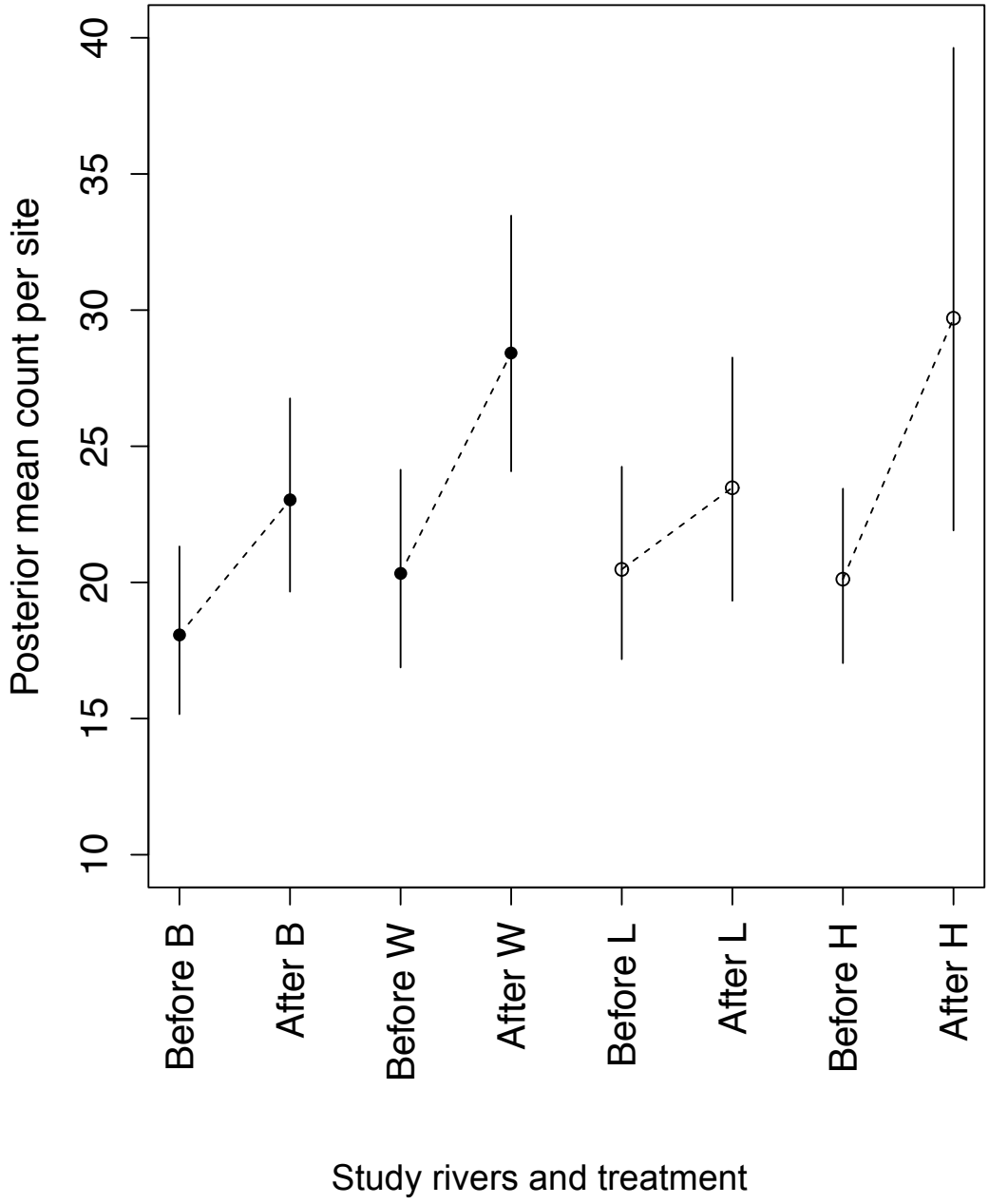


Figure 8. Posterior mean estimates of the before-after change in mean count per site of autumn 1+ salmonids for each river. Vertical lines are 95% Bayesian credible intervals. Open circles are control rivers, closed circles are flow-restored rivers. Horizontal line at zero change.

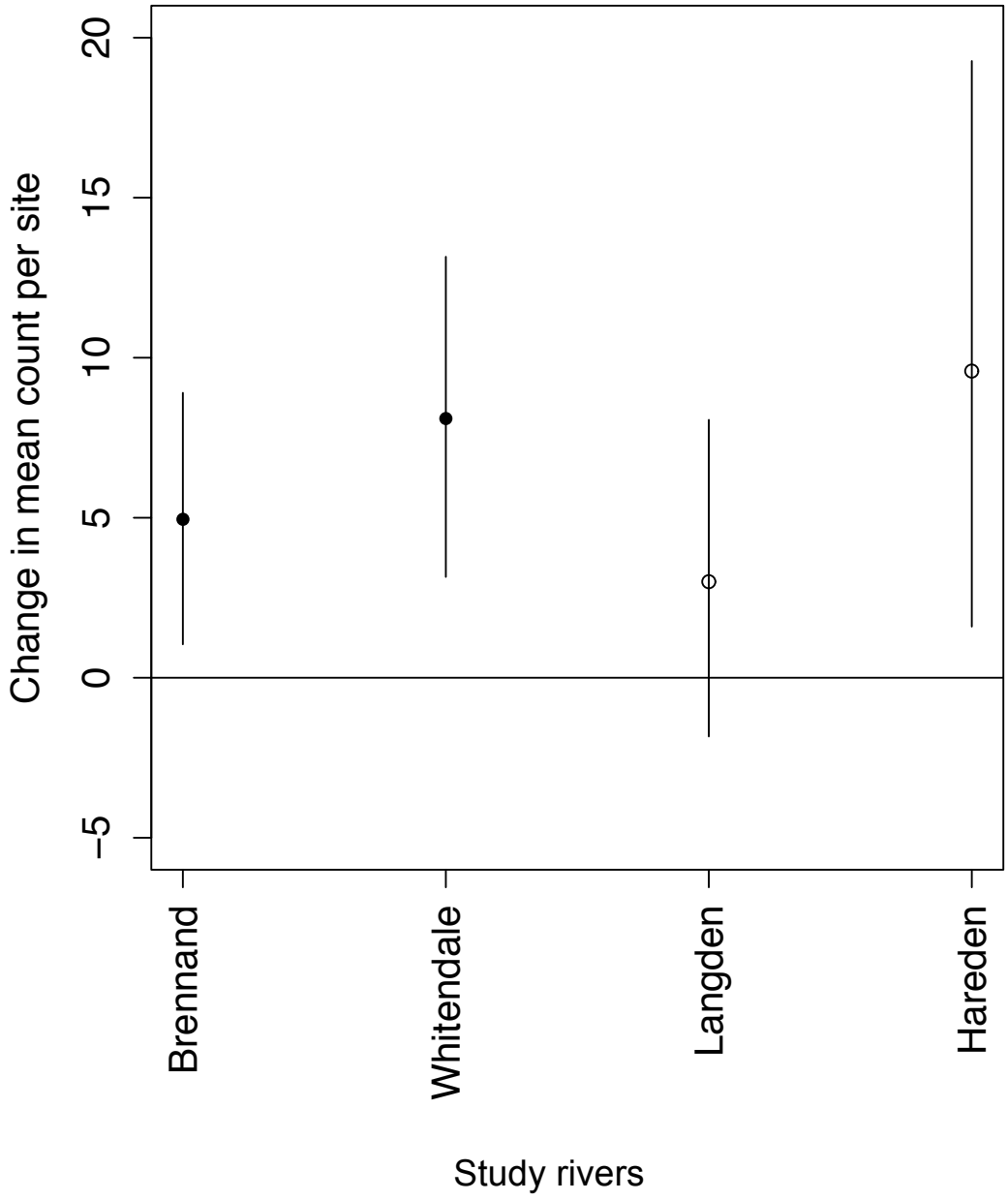


Figure 9. Posterior mean estimates of the differences in before-after changes in mean count per site of autumn 1+ salmonids between rivers. Vertical lines are 95% Bayesian credible intervals. Horizontal line at zero difference in change. Differences between each river: BW = Brennand and Whitendale, BL = Brennand and Langden, BH = Brennand and Hareden, WL = Whitendale and Langden, WH = Whitendale and Hareden, LH = Langden and Hareden.

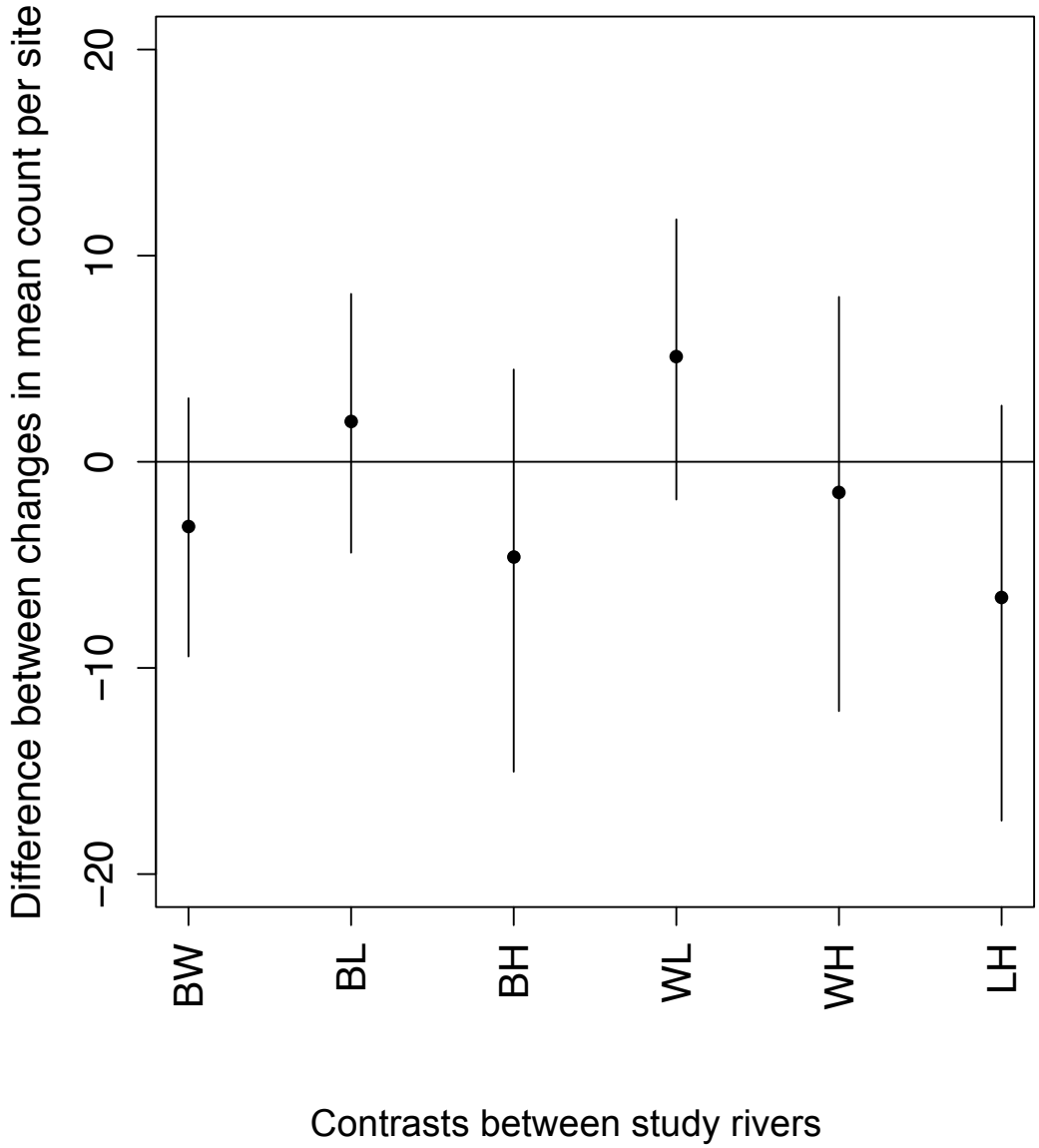


Figure 10. Posterior mean estimates of differences in mean count per site of autumn 1+ salmonids between rivers for the before period. Vertical lines are 95% Bayesian credible intervals. Horizontal line at zero change. Differences between each river: BW = Brennand and Whitendale, BL = Brennand and Langden, BH = Brennand and Hareden, WL = Whitendale and Langden, WH = Whitendale and Hareden, LH = Langden and Hareden.

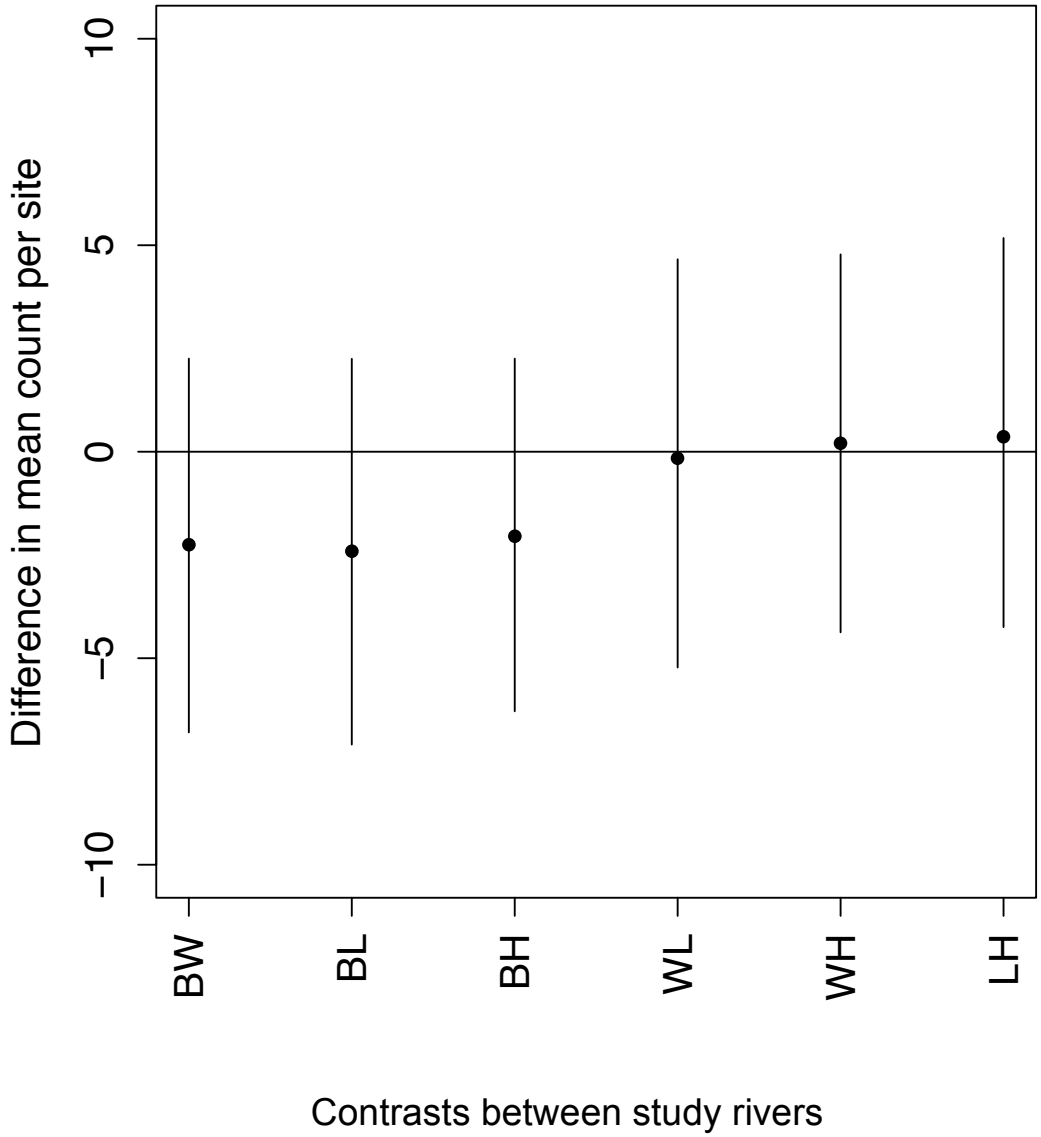


Figure 11. Posterior mean estimates of differences in mean count per site of autumn 1+ salmonids between rivers for the after period. Vertical lines are 95% Bayesian credible intervals. Horizontal line at zero change. Differences between each river: BW = Brennand and Whitendale, BL = Brennand and Langden, BH = Brennand and Hareden, WL = Whitendale and Langden, WH = Whitendale and Hareden, LH = Langden and Hareden.

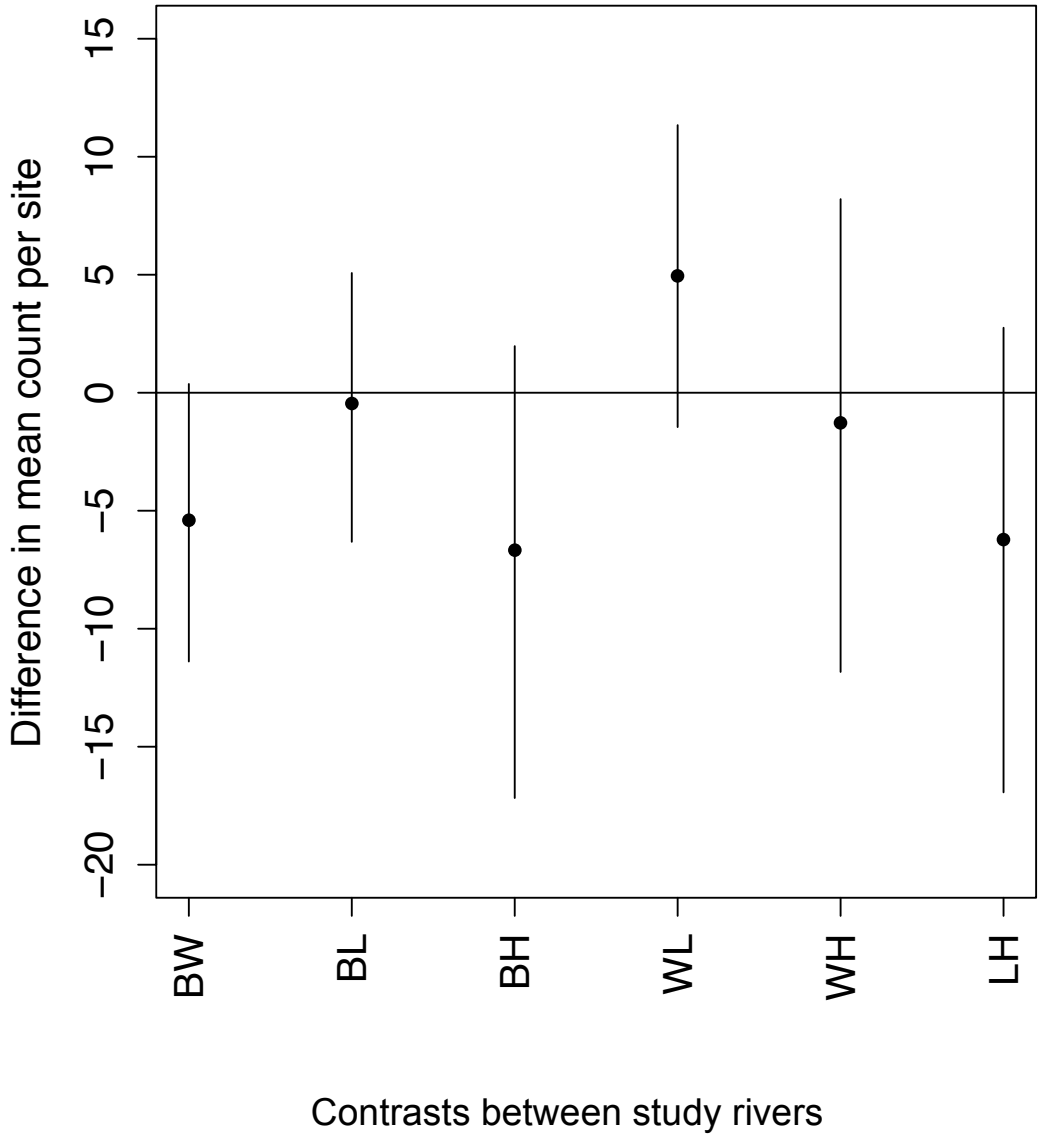


Figure 12. Variogram of residuals from the 0+ salmonid model for the River Brennand. Explain.

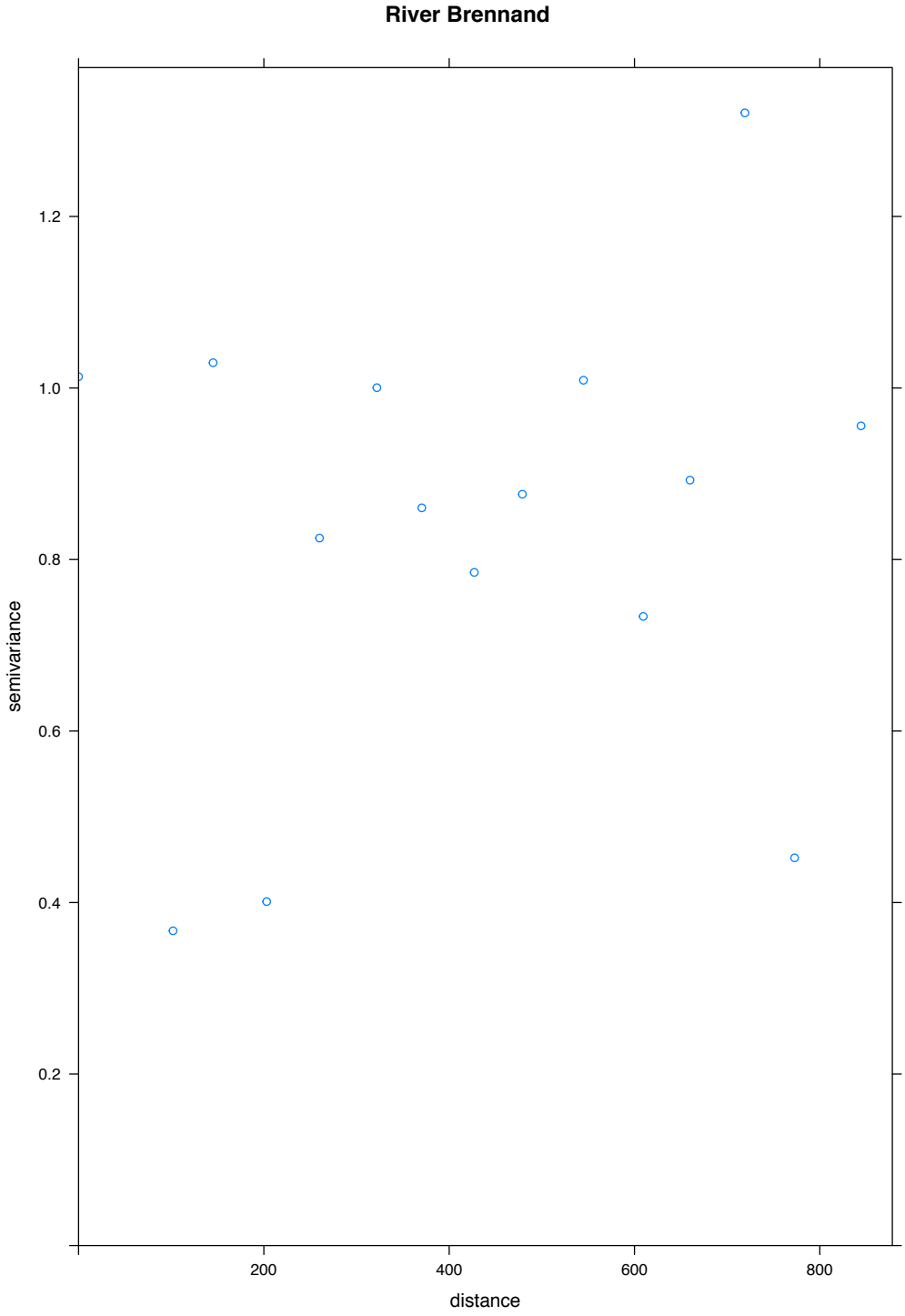


Figure 13. Variogram of residuals from the 0+ salmonid model for the River Whitendale. Explain.

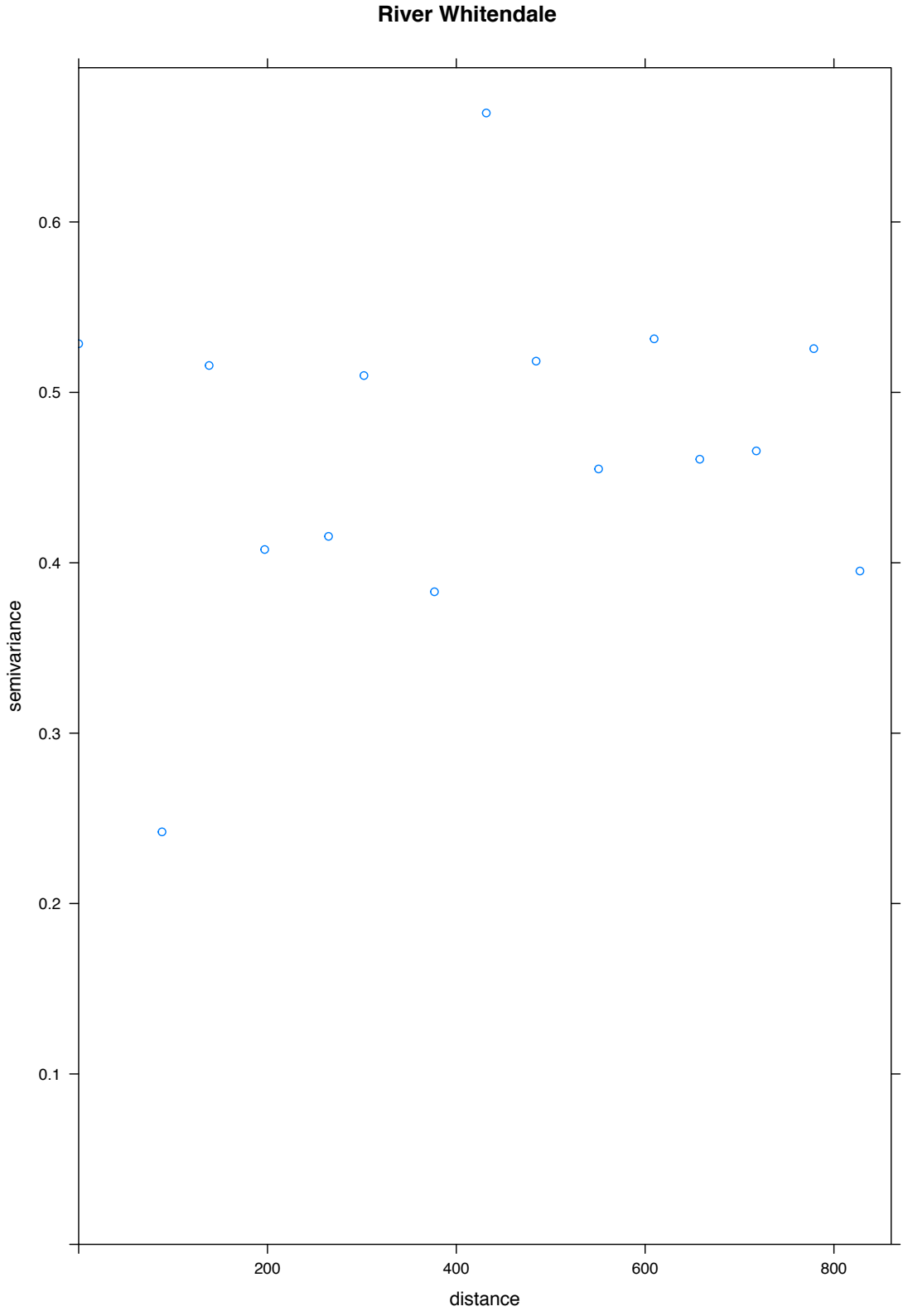


Figure 14. Variogram of residuals from the 0+ salmonid model for the River Langden. Explain.

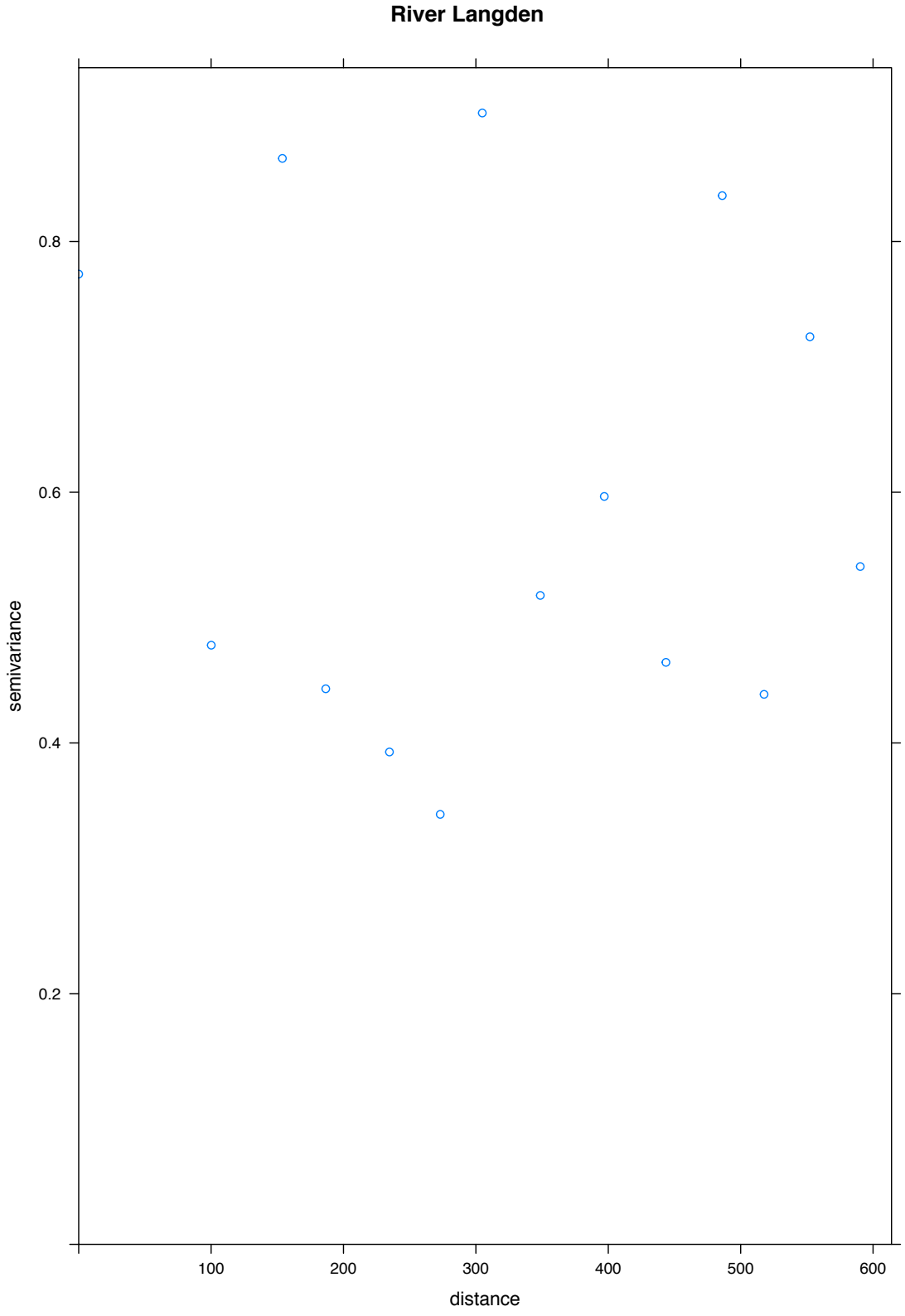


Figure 15. Variogram of residuals from the 0+ salmonid model for the River Hareden. Explain.

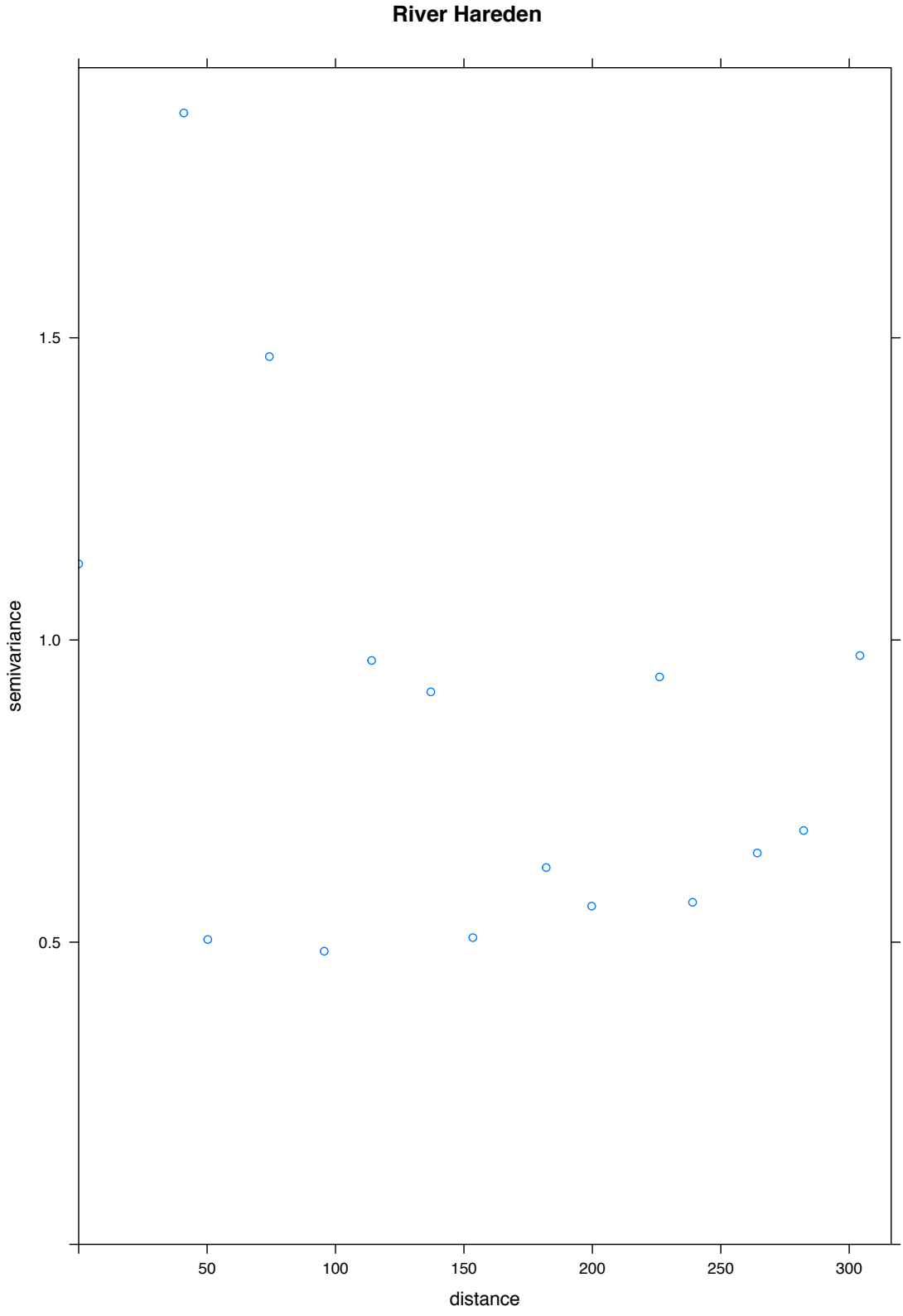


Figure 16. Out of sample prediction results for the 0+ negative binomial model. Each panel represents one omitted count of 0+ salmonids. The posterior mean distribution obtained from the model is shown for each panel. The red dot is the actual omitted count.

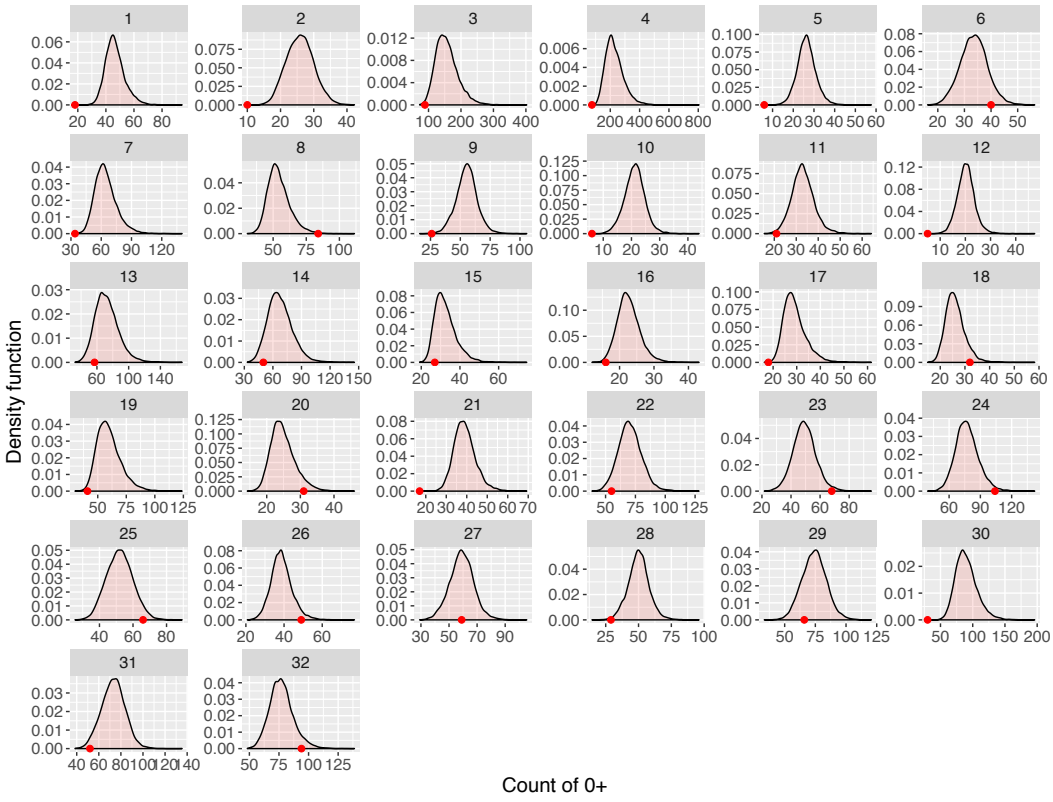
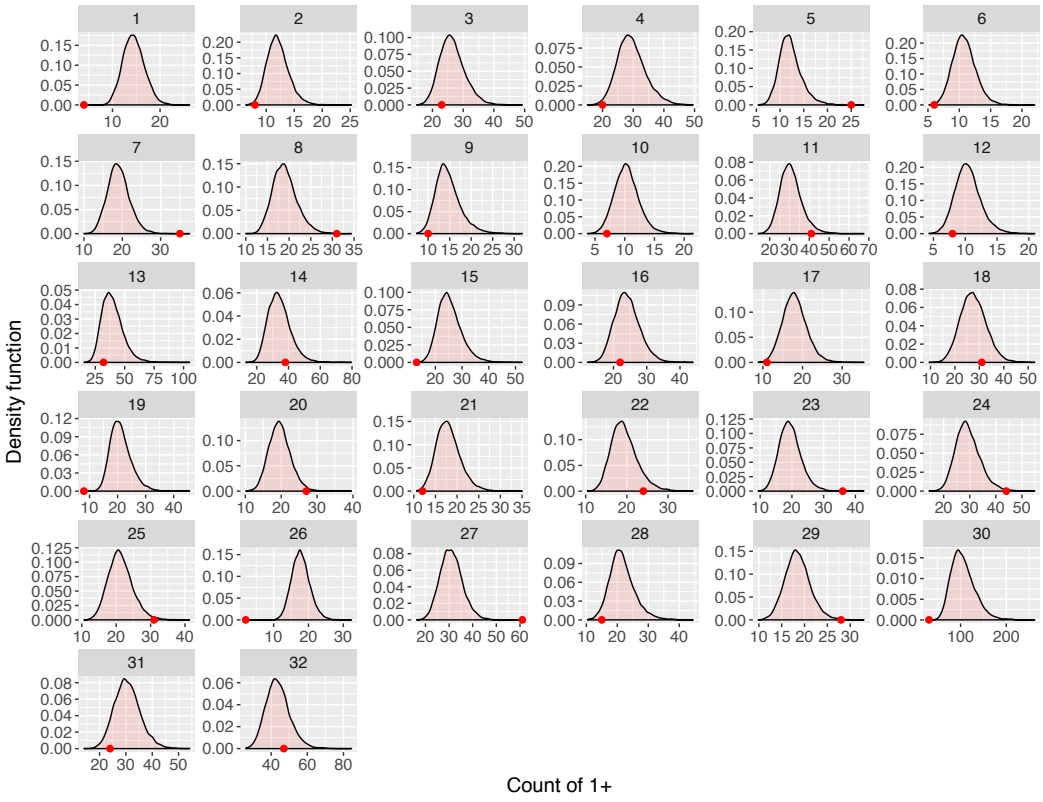


Figure 17. Out of sample prediction results for the 1+ negative binomial model. Each panel represents one omitted count of 1+ salmonids. The posterior mean distribution obtained from the model is shown for each panel. The red dot is the actual omitted count.



Chapter Six

THE GROWTH OF JUVENILE BROWN TROUT IN RESPONSE TO RIVER FLOW RESTORATION

ABSTRACT

Negative anthropogenic impacts on rivers have led to attempts to restore the biotic integrity of river systems using a variety of approaches. I investigated the effects of flow restoration on the mean growth rate of 0+ and 1+ brown trout (*Salmo trutta*) in upland rivers in northern England that have historically experienced low summer flow as a result of impoundment and water abstraction. Fish growth is indeterminate and flexible and is highly sensitive to environmental change. As such, growth rate is an appropriate variable for measuring short-term and fine-scale responses to habitat or river flow restoration. Four rivers were surveyed in a Before-After-Control-Impact (BACI) design, with two rivers undergoing summer flow restoration and two acting as controls. Summer and autumn electrofishing surveys were conducted on all rivers between 2011-2014. Flow restoration was implemented on the two restored rivers in 2012. Growth rates were estimated using length-frequency analysis. Bayesian GLMMs were used to test for the effects of flow restoration on the mean growth rate of 0+ and 1+ brown trout. Evidence for important benefits of flow restoration on the growth rates of 0+ and 1+ brown trout at restored rivers in comparison with control sites was evident, with clear improvement to growth performance immediately following implementation of flow restoration schemes. The study highlights a need for the selection of appropriate response variables and a rigorous statistical approach to site selection and study design in order to assess the effectiveness of river flow restoration measures. River flow

restoration studies often produce monitoring data that are unbalanced, have highly skewed non-normal response variables and inherent dependency. I demonstrate the effectiveness of Bayesian GLMMs for analysing data from such studies and discuss the implications of the results in the context of water resource and river management.

INTRODUCTION

River flow regime impinges on a number of key aquatic processes, including dissolved oxygen concentration, sediment transport and deposition, water quality, and habitat type and distribution (Poff et al., 1997; Richter et al., 1998; Bunn and Arthington, 2002; **Chapter 1**). An outcome is that river flow variation influences the spatial and temporal distribution of a broad range of aquatic biota, including fish (Jowett et al., 2005; Poff and Zimmerman, 2010). Human demands placed on water resources can result in the disruption of natural river flows, either through extracting water, regulating rivers using weirs and dams, or indirectly by altering run-off through changing land use (Freeman et al., 2001; Cattanéo, 2005; Park et al., 2006; Benejam et al., 2010). Understanding the relationship between river flow and discharge, water abstraction and fish abundance and distribution represents a major goal of aquatic ecology and fisheries management, and particularly for river rehabilitation and restoration (Richter et al., 2003; Souchon et al., 2008; Poff et al., 2010; **Chapter 1**).

Salmonid fishes serve as suitable models for understanding the impact of changes to river flow regime (Armstrong et al., 1998; Connor et al., 2003; Jager and Rose, 2003; Beechie et al., 2006; Nislow and Armstrong, 2012). Salmonid fishes are key components of freshwater systems and are of commercial interest in fisheries and aquaculture. Many populations of salmonids are migratory, occupying entire river

catchments, from headwaters to estuaries, making them particularly sensitive to river flow regime alteration. As such, salmonids have been considered good ecological indicators of the impact of flow regime on ecosystems over a broad range of environmental scales (Milner et al., 2012; Nislow and Armstrong, 2012; **Chapter 1**).

River restoration methods take a number of forms (see Roni et al., 2008 and Warren et al., 2015 for reviews) and are commonly based on a premise that that if habitat conditions are suitable, the biota will respond positively, an approach termed the 'Field of Dreams Hypothesis'; "if you build it, they will come" (Palmer et al., 1997). Despite its obvious shortcomings, this approach is often advocated on the basis that a lack of knowledge in quantifying biological processes should not be a barrier to action. A more rational approach, termed 'process-based restoration' (Beechie et al. 2010), is to employ habitat restoration and rehabilitation measures alongside the activities of ecologists that have both field and quantitative skills to design restoration measures, implement monitoring protocols and, what has hitherto been a significant omission, to devise appropriate statistical analyses to demonstrate ecological benefits (Warren et al., 2015). However, while the importance of pre- and post-restoration monitoring is widely acknowledged (though not always implemented) (Beechie et al. 2010), identifying what response variable is most relevant to measure the success of flow restoration schemes is often opaque (Warren et al., 2015). In most cases the abundance of a single (or multiple) focal species is used as a measure of restoration success (Roni et al., 2008; Beechie et al. 2010). However, whether this approach is the most appropriate remains to be validated (Warren et al., 2015; **Chapter 1**).

An alternative approach to using a demographic response to restoration is to examine the consequences for key life-history traits, such as reproduction (Wang et al.,

2014; King et al., 2015) or growth (Sommer et al., 2001; Phelps et al., 2015). Reproductive parameters, including fecundity, egg survival and egg quality, as well as somatic growth are highly responsive to environmental change (Wootton, 1998; Wootton and Smith, 2015). As such, these variables provide potential scope for measuring responses to habitat change with greater precision, and on a finer temporal scale than demographic parameters. Growth in fishes is particularly sensitive to environmental change because, with few exceptions, growth is indeterminate and highly flexible (Wootton, 1998). While growth rates reflect endogenous factors, they are strongly dictated by the environment, either through food availability, water quality, temperature, and hydraulic regime (Wootton, 1998). Growth can be readily measured in natural populations of fish based on changes in weight or length combined with age data derived from ageing fish using calcareous structures, such as scales and otoliths, which show distinct annual patterns. Robust bioenergetics models of fish growth have also been characterised, such as the von Bertalanffy growth model, which enable fish growth to be described and predicted (Helser and Lai, 2004; Katsanevakis, 2006).

The Environment Agency of England (EA) implemented a national Restoring Sustainable Abstraction (RSA) programme in the late 1990s to tackle perceived ecological problems arising from water abstraction and impoundments. In the North West region of England, the EA undertook a multiple catchment RSA study with the water company United Utilities (UU) to quantify the ecological benefits of altering water abstraction and restoring river flow regimes to a less altered state (see **Chapter 5** for details). For salmonids, the early life stages (0+ and 1+ age classes) were targeted, since these were the most abundant age classes and were judged most susceptible to

alterations in flow regime due to their limited capacity to move large distances (Environment Agency, 2009; Milner et al., 2012; Warren et al., 2015; **Chapter 5**).

The inference of any ecological response to river flow alteration can be problematic to demonstrate and requires a specific experimental design paired with an appropriate statistical model. The Before-After-Control-Impact (BACI) design is one that is often employed, thereby controlling for temporal and spatial effects (Stewart-Oaten et al., 1986; Underwood, 1992; Smith, 2002), see **Chapter 4** for a fuller consideration of BACI designs.

An additional consideration is the response variable within the chosen statistical framework. The response variable for models in this chapter is mean growth rate, which as it is measured here, is a strictly positive integer where the presence of zero is highly unlikely. I have measured growth as a function of change in length, and as such, negative values are not possible (Wootton, 1998). Hence, due to the nature of the growth rate response variable the most suitable distribution was a gamma distribution (Bolker et al., 2009; Zuur et al., 2009).

The goal of the present study was to use Bayesian GLMMs to assess the results of a controlled study focused on four rivers, two of which underwent flow restoration within the North West RSA study. An assumption was that provision of a more 'natural' summer low flow to rivers that had previously experienced high abstraction levels should benefit 0+ and 1+ salmonid fishes (Environment Agency, 2009), thereby providing evidence for a direct benefit of flow restoration for salmonids in upland rivers in the UK. In particular, I ask whether flow restoration can have detectable effects on the mean growth rate of juvenile brown trout (*Salmo trutta*).

METHODS

For details of study area, water abstraction and study design, see **Chapter 5**. For the present study only data for 0+ and 1+ brown trout were examined. Atlantic salmon (*Salmo salar*) were excluded from the analysis because these fish are wholly migratory and express a different growth trajectory to that of trout (Eggilshaw and Shackley, 1977). Additionally, salmon were found in low numbers at one control river and were absent from the other control river. These relatively sparse data make some analyses, such as modal length progression analysis, unreliable (Gayanilo and Pauly, 1997).

Estimating growth rate

Fish mean growth rates were estimated by length-frequency analysis using the *FSA* package ver. 0.6.13 (Ogle, 2016a) in the R statistical environment, ver. 3.2.3 (R Development Core Team, 2016). Length-frequency analysis is a method frequently applied to fisheries data that relies on the study population having a seasonal reproductive cycle so that recruitment to the population occurs approximately annually (Gayanilo and Pauly, 1997). If reproduction occurs discretely and annually then age cohorts form distinct modes in a size-frequency distribution. If length-frequency data are collected at known intervals of time, the shift in size of a particular cohort, termed modal progression, can be estimated under an assumption that the shift arises from an increase in length of the fish in the cohort over time (Wootton, 1998; Ogle, 2016b). Growth was estimated by modal progression and represents an estimate of mean growth rate between two within year sampling periods in mm per day, referred to as *g*0+ and *g*1+ for each age class respectively.

Data treatment and statistical models

Data exploration was undertaken following the protocol of Zuur et al. (2010) to examine the data for outliers in the response and explanatory variables, homogeneity and zero inflation in the response variable, collinearity between explanatory variables and the nature of relationships between the response and explanatory variables. The only potential concerns were the reduced number of surveys at the River Hareden (control) in Autumn 2013 and 2014 and the River Langden (control) in Autumn 2014 due to severe weather, which resulted in some imbalance in the data for those years.

Generalised linear mixed models (GLMMs) were fitted to the estimated posterior mean growth rate of each juvenile age class (0+ and 1+). To test for a period effect (Before/After flow restoration) on mean growth rate the following Gamma GLMM was fitted to data for each age class:

$Growth_{ijk} \sim Gamma(\mu_{ijk}, \tau)$

$E[Growth_{ijk}] = \mu_{ijk}$

$\text{var}(Growth_{ijk}) = \mu_{ijk}^2/\tau$

τ is the shape and scale parameter within the gamma distribution

$\log(Growth_{ijk}) = \eta_{ijk}$

$Growth_{ijk}$ = the kth observation of mean growth rate during period i in river j for site k

where period (i) = 1…2

river (j) = 1…4

site (k) = 1…69

$$\eta_{ijk} = \beta_1 + \beta_2 \text{ x } Ndate1_{ijk} + \beta_3 \text{ x } Period_i + \beta_4 \text{ x } River_j + \beta_5 \text{ x } Ndate1_{ijk} \text{ x } Period_i +$$

$$\beta_6 \text{ x } N_{date1ijk} \text{ x } River_j + \beta_7 \text{ x } Period_i \text{ x } River_j + \beta_8 \text{ x } _{Ndate1ijk} \text{ x } Period_i \text{ x } River_j + \quad a_k$$

$$+ b_k * N_{date1ijk}$$

$$a_k = N(0, \sigma^2)$$

$$b_k = N(0, \sigma^2)$$

where η_{ijk} contains 8 parameters consisting of main terms (Intercept, N_{date1}, Period, River) and 2-way interaction terms (N_{date1} x Period, N_{date1} x River, Period x River) and a 3-way interaction (N_{date1} x Period x River).

N_{date1} = standardised number of fish at sampling date 1

Period = 2 level factor (Before or After flow restoration)

River = 4 level factor (Brennand, Whitendale, Langden, Hareden)

In addition to period effects, I also examined the between year variation in growth rate within and among rivers. My *a priori* prediction was that the growth rate of each age class would vary among years and that this variation might mask any period effects when averaging year-to-year growth rate over a period. To quantify between year variation in mean growth rate the following Gamma GLMM was fitted to data for each age class:

$$Growth_{ijk} \sim Gamma(\mu_{ijk}, \tau)$$

$$E[Growth_{ijk}] = \mu_{ijk}$$

$\text{var}(Growth_{ijk}) = \mu_{ijk}^2/\tau$

τ is the shape and scale parameter within the gamma distribution

$\log(Growth_{ijk}) = \eta_{ijk}$

$Growth_{ijk}$ = the kth observation of mean growth rate during year i in river j for site k

where year (i) = 1…4

river (j) = 1…4

site (k) = 1…69

$$\eta_{ijk} = \beta_1 + \beta_2 \text{ x } N_{date1ijk} + \beta_3 \text{ x } Year_i + \beta_4 \text{ x } River_j + \beta_5 \text{ x } N_{date1ijk} \text{ x } Year_i + \beta_6 \text{ x } N_{date1ijk} \text{ x } River_j + \beta_7 \text{ x } Year_i \text{ x } River_j + \beta_8 \text{ x } N_{date1ijk} \text{ x } Year_i \text{ x } River_j + a_k + b_k * N_{date1ijk}$$

$a_k = N(0, \sigma^2)$

$b_k = N(0, \sigma^2)$

where η_{ijk} contains 8 parameters consisting of main terms (Intercept, N_{date1}, Year, River) and 2-way interaction terms (N_{date1} x Year, N_{date1} x River, Year x River) and a 3-way interaction (N_{date1} x Year x River).

N_{date1} = standardised number of fish at sampling date 1

Year = 4 level factor (2011, 2012, 2013, 2014)

River = 4 level factor (Brennand, Whitendale, Langden, Hareden)

In all cases models were fitted to the following response variables:

1. 0+ trout mean growth rate (g_{0+})
2. 1+ trout mean growth rate (g_{1+})

Exploratory data plots confirmed that the relationship between summer count (N_{date1}) and mean growth rate for each age class was different in each year and on each river and that there was considerable site-by-site variation in the relationship. I elected, *a priori*, to incorporate a fixed effect term for summer counts (N_{date1}) and a survey site random effect for N_{date1}, as confirmed by my data exploration. A random intercept and slope model permits both survey-site level random effects for summer counts and inherent temporal and spatial correlation at the survey site level.

Model parameters were estimated in a Bayesian framework (**Chapter 2**) using the *R2jags* package (Su and Yajima, 2012) in the R statistical environment (R Development Core Team, 2016). For each model three independent Markov chains were run simultaneously. A burn-in of 10,000, thinning rate of 10 and 50,000 iterations were used, which resulted in 12,000 Markov Chain samples for each estimated parameter. Mixing (stationarity) and autocorrelation of chains were checked visually using trace plots and the Gelman-Rubin statistic (Brooks and Gelman, 1998). Autocorrelation was low and convergence was achieved in each case. Model validation showed no evidence of heterogeneity or non-linear patterns in the model residuals (Zuur et al., 2013).

To investigate the effect of flow restoration on mean growth rate, model parameters were used to estimate the posterior mean growth rate of 0+ and 1+ trout given the summer count of trout (N_{date1}) for each river and period, and for each river and year with Bayesian 95% credible intervals. In order to examine how rivers differed in

mean growth rate between periods and between years, I estimated the difference in growth rate between periods and years for each river along the N_{date1} gradient.

Spatial correlation was assessed with the use of variograms that estimate and plot the semi-variance of model residuals against spatial coordinates (see Zuur et al., 2009, 2013 and 2014 for details) and showed that any residual spatial correlation was likely to be weak. Variograms for the 0+ model and 1+ model were similar to those for models in **Chapter 5** so are not shown for brevity. The goodness of fit for each model was assessed using an 'out of sample' prediction method (see **Chapters 3** & **4** for details). Graphical results of this method are given in **Figures 33** & **34**. The percentage of observed data points within the model estimated posterior mean distributions were 60% for the 0+ model and 41% for the 1+ model.

RESULTS

Model results

0+ trout growth rate before and after flow restoration

There was an apparent change in the relationship between N_{date1} and g_{0+} between periods for the River Brennand (**Figure 1**). In the before restoration period g_{0+} showed a density-dependent response, with g_{0+} decreasing with increasing N_{date1}, the posterior mean slope is -0.12 mm day^{-1} with no zero in the credible intervals (**Table 1**), while in the after restoration period there appears to be no effect of density (N_{date1}) on g_{0+}, the posterior mean slope is -0.02 mm day^{-1} and included zero in the credible interval (**Table 1**). The difference in the relationship between N_{date1} and g_{0+} between periods was only important at N_{date1} values of approximately 140 fish and above (**Figure 5**) and shows that the growth rate of 0+ trout (g_{0+}) had clearly increased at higher densities in the period after flow restoration.

The relationship between N_{date1} and g_{0+} in each period for the River Whitendale was similar to that for the River Brennand with a posterior mean slope of -0.08 mm day^{-1} in the period before flow restoration but with zero in the tail of the lower credible interval (**Table 1** and **Figure 2**). The observed negative relationship was weaker than that for the Brennand in the before restoration period. The N_{date1} and g_{0+} relationship for the Whitendale in the after flow restoration period is similar to that of the Brennand in the same period with a posterior mean slope of -0.05 mm day^{-1}, but with zero in the credible interval implying no effect of N_{date1} for the after flow restoration period (**Table 1** and **Figure 2**). There was no difference in the relationship between N_{date1} and g_{0+} between flow restoration periods (**Figure 6**) showing that there were broadly similar density-independent growth rates of trout for this river in each period.

There was an important positive relationship between N_{date1} and g_{0+} in the before period for the control River Langden (**Figure 3**) with a posterior mean slope of 0.17 mm day^{-1} and no zero in the credible interval (**Table 1**). This relationship was the converse to that seen in both flow restored rivers (**Figure 1** and **Figure 2**) and for the other control River Hareden (**Figure 4**) for the same period. In the after restoration period the relationship between N_{date1} and g_{0+} appeared to have changed to a negative relationship (**Figure 3**) with a posterior mean slope of -0.04 mm day^{-1} with a zero in the credible interval (**Table 1**). There was an important difference in the relationship between N_{date1} and g_{0+} between flow restoration periods, but only at lower N_{date1} values of approximately 70 fish or less (**Figure 7**), showing that the growth rate of 0+ trout (g_{0+}) had clearly increased at lower densities in the period after flow restoration.

The control River Hareden exhibited a negative relationship between N_{date1} and g_{0+} in both periods (**Figure 4**). The posterior mean slope for the before period was -0.10 and for the after period was -0.04 and with both slope estimates containing zeros in the credible intervals (**Table 1**). There was no difference in the N_{date1} and g_{0+} relationship between flow restoration periods (**Figure 8**), which showed that the growth rate of 0+ trout (g_{0+}) was similar in both flow restoration periods. For this river the effect of the reduction in data for years 2013 and 2014, the period after flow restoration, can be seen in the wide credible intervals (**Figure 4** and **Figure 8**).

1+ brown trout growth rate before and after flow restoration

The relationship between N_{date1} and g_{1+} in both flow restoration periods for the River Brennand was broadly similar (**Figure 9**). In the before period g_{1+} was clearly density-dependent and decreased with increasing N_{date1}, the posterior mean slope was -0.09 mm

day^{-1} with no zero in the credible intervals (**Table 2**), while in the after period there appeared to be no effect of N_{date1} on g_{1+}, the posterior mean slope remained at -0.09 mm day^{-1} but contained zero in the credible interval (**Table 2**). Although the N_{date1} and g_{1+} relationship was similar for each period, the growth rate of 1+ trout (g_{1+}) was clearly greater in the after flow restoration period at N_{date1} values between 50 and 150 fish (**Figure 13).**

The relationship between N_{date1} and g_{1+} in both flow restoration periods for the River Whitendale was broadly similar to that for the River Brennand (**Figure 10**). The postyerior mean slope for N_{date1} was -0.02 mm day^{-1} in the before period and -0.05 mm day^{-1} in the after period and both posterior mean slopes had zero in the credible intervals (**Table 2**), which implies that growth rate was not density-dependent in either period for this river. The difference in the growth rate of 1+ trout (g_{1+}) between periods was similar to that for the Brennand, with clearly greater g_{1+} in the after flow restoration period at N_{date1} values between 50 and 100 fish (**Figure 14).**

Like the result for 0+ growth rate (g_{0+}), there appeared to be a positive relationship between N_{date1} and g_{1+} in the before restoration period for the control River Langden (**Figure 11**), with a posterior mean slope of 0.15 mm day^{-1} but with zero in the credible interval (**Table 2**). In the after restoration period the relationship between N_{date1} and g_{1+} was negative with a posterior mean slope of -0.050 mm day^{-1}, but with zero in the credible interval (**Table 2** and **Figure 11**). These results suggest no relationship between N_{date1} and g_{1+} in either period thereby implying that growth rate was not density-dependent over the study period. Despite the lack of evidence for density-dependent growth for either period, there was clearly lower growth rate for 1+ trout (g_{1+}) in the after restoration period when N_{date1} was greater than 75 fish (**Figure 15**).

The control River Hareden exhibited a negative relationship between N_{date1} and g_{1+} in the before restoration period (**Figure 12**). The posterior mean slope for the before restoration period was -0.29 mm day^{-1} with no zero in the credible interval (**Table 2**), suggesting that 1+ trout growth rate was density-dependent in this period. In the after restoration period the posterior mean slope for g_{1+} was 0.14 mm day^{-1} but this slope estimate contained zeros in the credible intervals. The difference in the relationship between N_{date1} and g_{1+} between periods (**Figure 16**) showed that 1+ trout growth rate (g_{1+}) was lower in the after period at N_{date1} values of less than 70 fish but higher at N_{date1} values greater than 140 fish. However, the paucity of data for this river in the after flow restoration period (2013 and 2014) means that this estimated difference could be unreliable.

0+ trout growth rate among years

There was a negative relationship between N_{date1} and g_{0+} for the River Brennand in 2011 prior to flow restoration (**Figure 17**) suggesting a density-dependent effect on growth rate in that year. The posterior mean slope estimate for N_{date1} in this year was -0.16 mm day^{-1} but with an upper 95% credible interval of 0.02 mm day^{-1}, which suggests the N_{date1} effect on g_{0+} was not important (**Table 3**). None of the other years showed such a relationship and all appear to show density-independent growth rate (**Figure 17** and **Table 3**). Growth rate (g_{0+}) in 2014 appears to be greater on average than the other years with a posterior mean g_{0+} of 0.30 mm day^{-1} (**Figure 17**). When the differences in the relationship between N_{date1} and g_{0+} are considered between years it is clear that growth rate (g_{0+}) at lower starting densities (N_{date1}) was greater in 2011 than either 2012 or 2013, the latter year is one year after the flow restoration measures came into effect

(**Figure 21**). When 2011 and 2014 are compared (**Figure 21**) there was no difference in growth rate when N_{date1} was less than 100 fish, but at higher values of N_{date1} growth rate in 2014 was clearly greater than in 2011. **Figure 21** also shows that at mid values of N_{date1}, growth rate in 2012 was greater than 2013 but lower than 2014. Growth rates along the whole gradient of N_{date1} were significantly lower in 2013 than 2014. Overall this finding suggests that 2013, one year after flow restoration, was a particularly poor year for growth compared with the other years and that growth rate improved markedly in 2014.

For the River Whitendale the relationship between N_{date1} and g_{0+} was negative but not important (**Table 3**) in 2011 and 2013 suggesting density-independent growth of 0+ trout in these years (**Figure 18**). Growth rate in 2012 was also density-independent, while in 2014 there appeared to be a slight positive, but unimportant, effect of density (N_{date1}) on growth rate (g_{0+}) (**Figure 18** and **Table 3**). There was no clear difference in growth rate between years 2011, 2012 and 2013 (**Figure 22**) and between years 2012 and 2014. At higher values of N_{date1} there was an important difference in growth rate between years 2011 and 2014 and between 2013 and 2014 (**Figure 22**) implying that at higher densities growth rate was greater in 2014, two years after the flow restoration was completed.

The relationship between N_{date1} and g_{0+} at the control River Langden was independent of density in all years (**Figure 19** and **Table 3**). There were important differences in growth rate (g_{0+}) between 2011 and 2012 and between 2011 and 2013 at densities (N_{date1}) of less than 100 fish (**Figure 23**). Growth rates were similar between all remaining years (**Figure 23**).

At the control River Hareden the relationship between N_{date1} and g_{0+} in years 2011 and 2012 appear to have been density-dependent (**Figure 20**) but their mean slope estimates contain zero in their credible intervals (**Table 3**). The paucity of data for years 2013 and 2014 make inferences about growth rate difficult (**Figure 20**) and the extremely wide credible intervals suggest that any relationship was unlikely given the data. For years where more data were available (2011 and 2012) there was clearly no difference between the relationship between N_{date1} and g_{0+} (**Figure 24**). Comparisons between other years resulted in wide credible intervals, suggesting that there were no differences for those years (**Figure 24**).

1+ trout growth rate among years

There was a slight negative relationship between N_{date1} and g_{1+} for the River Brennand in all years prior to and following flow restoration (**Figure 25**) suggesting a consistent density-dependent relationship. However, the presence of zero in the credible intervals for these slope estimates means that there was an unimportant relationship between N_{date1} and g_{1+} (**Table 4**) and 1+ growth rate in this river was density-independent over the study years. When the relationship between N_{date1} and g_{1+} was compared between years, 2013, one year after flow restoration, showed an important greater growth rate than in 2011 for N_{date1} values of 50 fish or greater (**Figure 29**). Growth rates were also higher in 2013 than that in 2012 for N_{date1} values up to 100 fish and also higher than 2014 for N_{date1} values between 60 and 110 fish. This finding suggests that growth rates of 1+ trout in 2013 were generally higher than that for other years.

On the River Whitendale the relationship between N_{date1} and g_{1+} appeared negative in 2011, 2012 and 2013, suggesting density-dependent growth of 1+ trout in

these years (**Figure 26**), though zero in the credible intervals indicates that the relationship between N_{date1} and g_{1+} was density-independent in these years (**Table 4**). The estimate of g_{1+} in 2012 appeared to be positively related to N_{date1} (**Figure 26**), but this result was not important due to zero in the credible intervals (**Table 4**). A comparison of the growth rate between years shows that growth rate in 2011 was clearly lower than that for 2012 for a starting abundance (N_{date1}) of 60 fish or greater (**Figure 30**). Growth rate in 2013 was higher than in 2011 across the range of N_{date1} (**Figure 30**), higher than in 2012 for N_{date1} values of up to 70 fish, and higher than 2014 for N_{date1} values of between 20 to 120 fish. This result suggests that growth rates of 1+ trout in 2013 were higher than in other years.

From 2011 to 2013 the relationship between N_{date1} and g_{1+} at the control River Langden was weakly positive and in 2014 weakly negative (**Figure 27**) but mean estimates for the N_{date1} slopes contained zeros in the credible intervals (**Table 4**). The growth rate of 1+ trout was density-independent in all years of the study at this control river. A comparison of growth rates between years showed that in 2012 the growth rate of 1+ trout was higher than 2011 for N_{date1} values of 30 to 100 fish, higher than 2013 for N_{date1} values of 50 to 120 fish and higher than 2014 for N_{date1} values of greater than 100 fish (**Figure 31**). This result implies that for this river the growth rates of 1+ trout were clearly higher in 2012 than other years in the study.

The relationship between N_{date1} and g_{1+} at the second control River Hareden appeared to be negative in 2011 and 2012, while in 2013 and 2014 there appeared to be no relationship (**Figure 28**). The credible intervals of the slope estimates for 2012 to 2014 contained zero (**Table 4**) indicating density-independent growth of 1+ trout in those years for this river. However, in 2011 the estimated slope for N_{date1} (-0.44 mm

day^{-1}) did not contain zero in the credible interval, so there was important density-dependent growth in that year. Due to the paucity of data for this river in 2013 and 2014 the only between year difference in growth rate that was considered robust was between 2011 and 2012 (**Figure 32**). For N_{date1} values of 60 fish and above the growth rate of 1+ trout was clearly higher in 2012 than 2011.

DISCUSSION

The goal of the present study was to assess the short-term effectiveness of flow restoration measures on the mean growth rate of juvenile brown trout in two upland rivers in the UK. Four rivers were surveyed in a Before-After-Control-Impact (BACI) design, with two rivers undergoing flow restoration and two acting as control rivers (see **Chapter 5** for full background to the study). The evidence demonstrating short-term benefits of flow restoration on juvenile brown trout growth rate was positive, although limited to some extent by a lack of data for the control rivers in 2013 and 2014. Broadly, my models demonstrate that over the four-year monitoring period, the mean growth rates of juvenile brown trout in the Rivers Brennand and Whitendale were enhanced in relation to flow restoration when compared with the control rivers Langden and Hareden over the same period. Both the restored rivers showed similar differences in juvenile growth rates between periods in a positive direction, while the control rivers shared similar differences between periods that were not positive. Within my broader results there were notable river and age class-specific differences in growth rate changes over the study period.

Some of my findings suggest that flow restoration may have provided a short-term benefit to 0+ brown trout in the River Brennand, but little benefit in the River

Whitendale. Growth rate of 0+ brown trout in the River Brennand was clearly enhanced in the period after flow restoration at higher levels of abundance. This finding implies that flow restoration on the River Brennand could have countered the density-dependent growth rate observed in the period before flow restoration. Such a change was not observed for either of the control Rivers Langden and Hareden. The observed change on the River Langden was the inverse of that observed on the Brennand with an important positive density-dependent growth rate occurring in the period before restoration followed by density-independent growth rate in the after period. When the changes observed in these rivers are considered on a yearly basis a noteworthy pattern emerges, which could be related to drought and abstraction induced density-dependent growth rate. Many parts of England experienced the driest 18 months for over 100 years between September 2010 and March 2012, with many rivers, including those in this study, classed as 'in drought' by the Environment Agency (Environment Agency, 2015). Juvenile trout growth rates in 2011 included drought conditions and this was the only year in the study where such conditions prevailed in the summer growth season. Extreme low flows are likely to reduce wetted habitat for riverine biota (Bunn and Arthington, 2002; **Chapter 1**), including trout and can lead to localised increases in the density of competing individuals. Under such conditions growth rates are likely to be supressed with potentially strong density-dependent effects (Crisp, 1993; Elliott, 1995; Nislow et al., 2004).

The control Rivers Langden and Hareden did not exhibit density-dependent growth for 0+ brown trout, indeed the River Langden showed significant density-independent growth. The control sites had water abstraction intakes, but these were located at the lower end of the rivers, downstream of reaches used by juveniles. This

finding implies that the controls, although abstracted and experiencing drought in 2011, most likely had sufficient flow and physical habitat to buffer the effects of drought-induced low flows on the growth rate of trout. Drought-induced flows coupled with water abstraction from the intake at the upper reach of the River Brennand may have led to more extreme low flows for fish thereby driving density-dependent growth in 0+ brown trout. It should be noted that the control rivers do not support Atlantic salmon, unlike the Rivers Brennand and Whitendale, and the absence of another salmonid species with similar juvenile habitat requirements may also explain the lack of density-dependent growth observed in the controls. A potential criticism of the present study is in the choice of control rivers, a point already discussed in **Chapter Five**, and relevant to the findings here.

My analysis shows that the changes in mean growth rate of juvenile trout in the Rivers Brennand and Whitendale provides evidence that water abstraction was negatively impacting this aspect of juvenile trout biology, and more than likely that of salmon given their similar habitat requirements for growth (Milner et al., 2003). Despite the limited evidence demonstrated in **Chapter Five** on the effects of abstraction and flow restoration on juvenile salmonid abundance, the results of the present chapter suggest that environmental managers and fishery scientists might think beyond variables such as abundance as restoration and conservation end points. Although more water may not equal more fish (**Chapter 5**, Bradford et al., 2011), more natural river flows that are timed to match critical growth periods may result in larger, more robust juveniles that successfully reach the smolt stage and then negotiate the various environmental pressures during migration to sea (Nislow and Armstrong, 2012). Resilience in salmonid populations may not simply be measured by abundance but

rather by meaningful measures of fitness (Nagrodski et al., 2012; Nislow and Armstrong, 2012; Richard et al., 2013), and these require appropriate monitoring so that parameters, such as growth rate used in this study, can be assessed. Indeed, whether the effects demonstrated in the present short-term study will persist in the longer-term will require such monitoring to continue.

While mean growth rates proved a promising variable on which to focus in this analysis, other variables might also have utility and may prove superior for monitoring. Thus, reproductive parameters have direct implications for population recovery and persistence (Wootton and Smith, 2015). There is a limited, but growing body of literature that recognises the implications of reproductive parameters for flow management (Dudley and Platania, 2007; Craven et al., 2010; King et al., 2010, 2016). Appropriate reproductive variables might include female fecundity, egg number, egg size, and larval abundance. Further studies to explore the utility of growth and reproductive parameters in measuring the success of river management, conservation and restoration measures are recommended.

Bayesian GLMMs again proved their utility in the current analysis for successfully dealing with a relatively complex dataset, and specifically in handling unbalanced nested data that showed an inherent lack of dependency due to repeated measures at sampling sites, and a highly varied non-normal response variable (fish mean growth rate). Bayesian GLMMs and similar models are powerful tools for ecological studies and environmental impact assessments and they should become the default for ecologists and environmental managers (Ellison, 1996; **Chapter 7**).

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TABLES

Table 1. Posterior mean slope estimates and 95% credible intervals for the N_{date1} effect on g_{0+} in each river and period. CrI is the 95% Bayesian credible interval.

River	Period	Posterior mean	Lower CrI	Upper CrI
Brennand	Before	-0.12	-0.16	-0.07
	After	-0.02	-0.10	0.06
Whitendale	Before	-0.08	-0.17	0.00
	After	-0.05	-0.18	0.08
Langden	Before	0.17	0.03	0.32
	After	-0.04	-0.23	0.14
Hareden	Before	-0.10	-0.23	0.03
	After	-0.04	-0.29	0.21

Table 2. Posterior mean slope estimates and 95% credible intervals for the N_{date1} effect on g_{1+} in each river and period. CrI is the 95% Bayesian credible interval.

River	Period	Posterior mean	Lower CrI	Upper CrI
Brennand	Before	-0.09	-0.15	-0.04
	After	-0.09	-0.18	0.01
Whitendale	Before	-0.02	-0.13	0.08
	After	-0.05	-0.20	0.10
Langden	Before	0.15	-0.02	0.32
	After	-0.05	-0.27	0.16
Hareden	Before	-0.29	-0.45	-0.13
	After	0.14	-0.15	0.42

Table 3. Posterior mean slope estimates and 95% credible intervals for the N_{date1} effect on g_{0+} in each river and year. CrI is the 95% Bayesian credible interval.

River	Year	Mean	Lower CrI	Upper CrI
Brennand	2011	-0.16	-0.33	0.02
	2012	-0.02	-0.20	0.17
	2013	-0.02	-0.21	0.18
	2014	-0.01	-0.20	0.17
Whitendale	2011	-0.11	-0.60	0.39
	2012	0.00	-0.51	0.51
	2013	-0.13	-0.63	0.38
	2014	0.06	-0.44	0.56
Langden	2011	0.28	-0.07	0.63
	2012	0.04	-0.27	0.35
	2013	-0.08	-0.39	0.21
	2014	0.01	-0.28	0.30
Hareden	2011	-0.10	-0.36	0.17
	2012	-0.10	-0.38	0.18
	2013	0.02	-0.57	0.59
	2014	0.06	-1.00	1.09

Table 4. Posterior mean slope estimates and 95% credible intervals for the N_{date1} effect on g_{1+} in each river and year. CrI is the 95% Bayesian credible interval.

River	Year	Posterior mean	Lower CrI	Upper CrI
Brennand	2011	-0.11	-0.29	0.06
	2012	-0.04	-0.23	0.15
	2013	-0.08	-0.29	0.11
	2014	-0.08	-0.27	0.10
Whitendale	2011	-0.02	-0.57	0.52
	2012	0.12	-0.43	0.69
	2013	-0.06	-0.61	0.49
	2014	-0.01	-0.57	0.54
Langden	2011	0.12	-0.29	0.53
	2012	0.05	-0.31	0.41
	2013	0.02	-0.31	0.35
	2014	-0.09	-0.42	0.23
Hareden	2011	-0.44	-0.74	-0.14
	2012	-0.19	-0.52	0.12
	2013	0.14	-0.53	0.83
	2014	-0.01	-1.27	1.24

FIGURES

Figure 1. Fitted values for 0+ brown trout posterior mean growth rate as a function of density before and after flow restoration for the River Brennand modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals. Note different scaling of axes for periods.

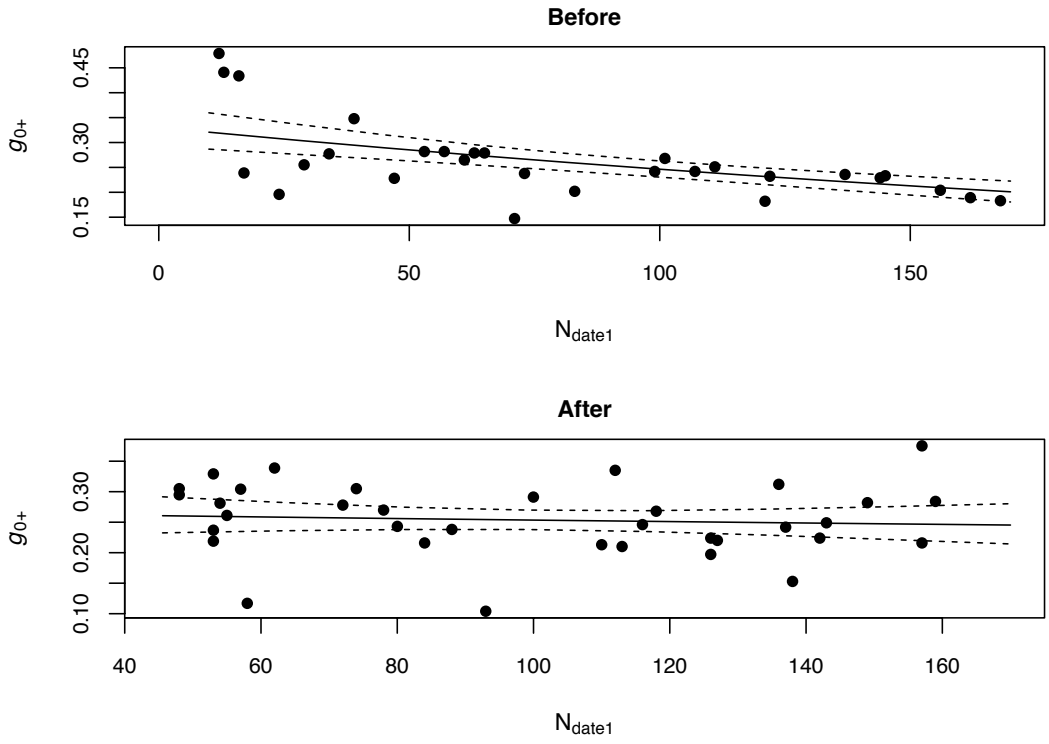


Figure 2. Fitted values for 0+ brown trout posterior mean growth rate as a function of density before and after flow restoration for the River Whitendale modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals. Note different scaling of axes for periods.

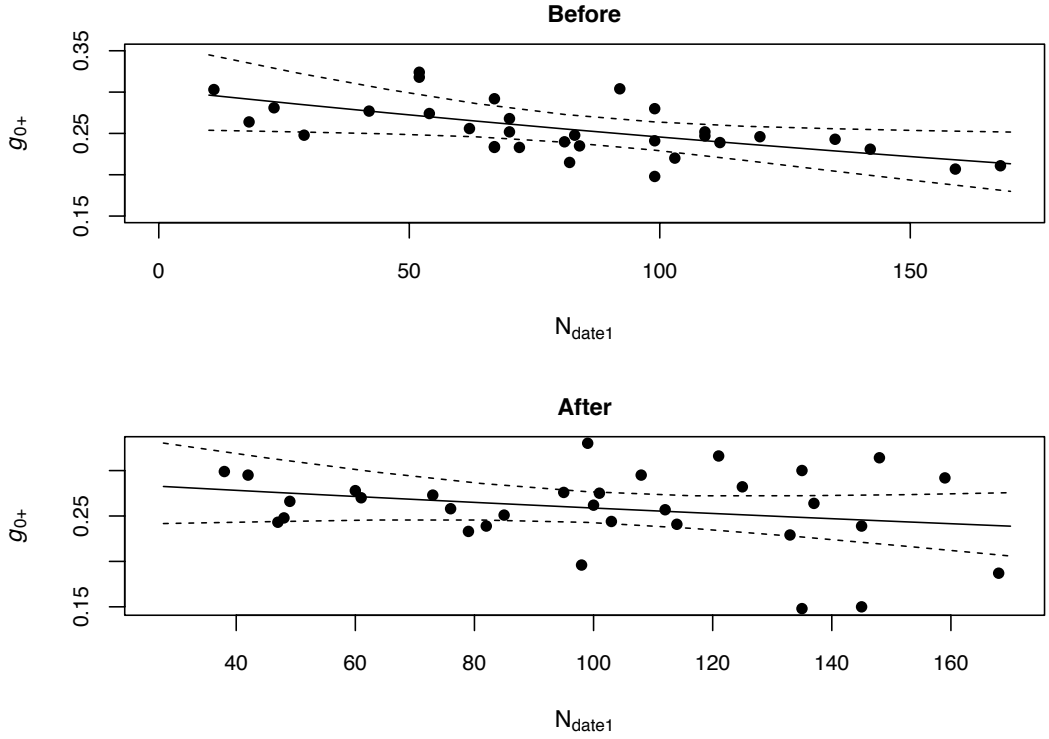


Figure 3. Fitted values for 0+ brown trout posterior mean growth rate as a function of density before and after flow restoration for the River Langden modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals. Note different scaling of axes for periods.

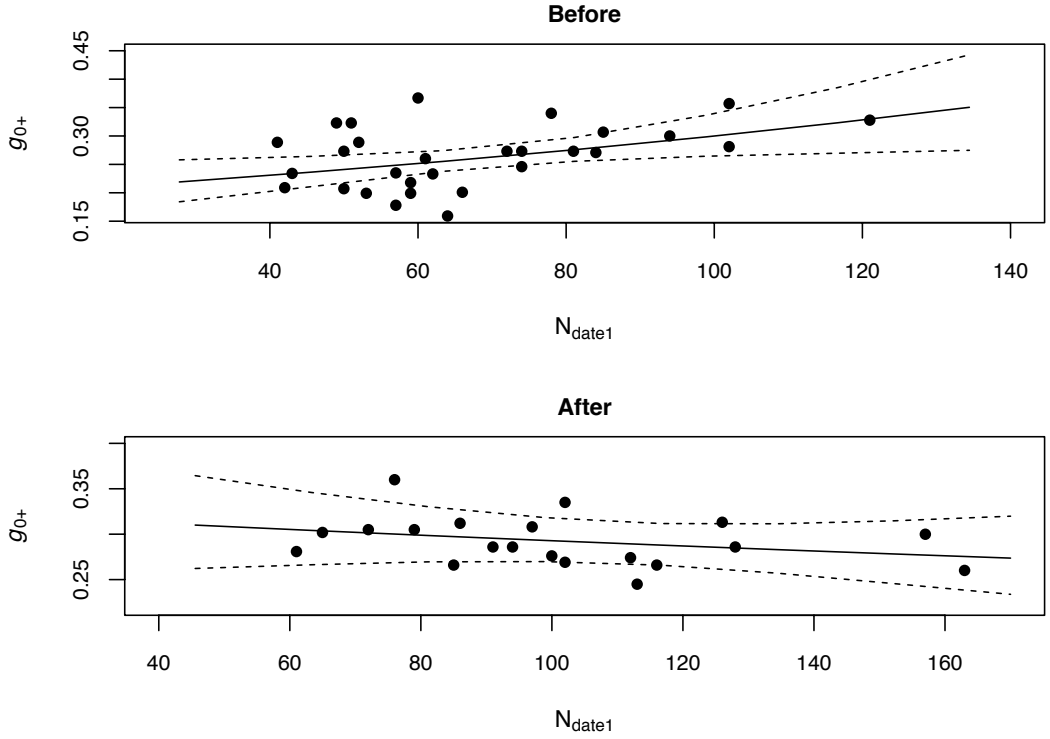


Figure 4. Fitted values for 0+ brown trout posterior mean growth rate as a function of density before and after flow restoration for the River Hareden modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals. Note different scaling of axes for periods.

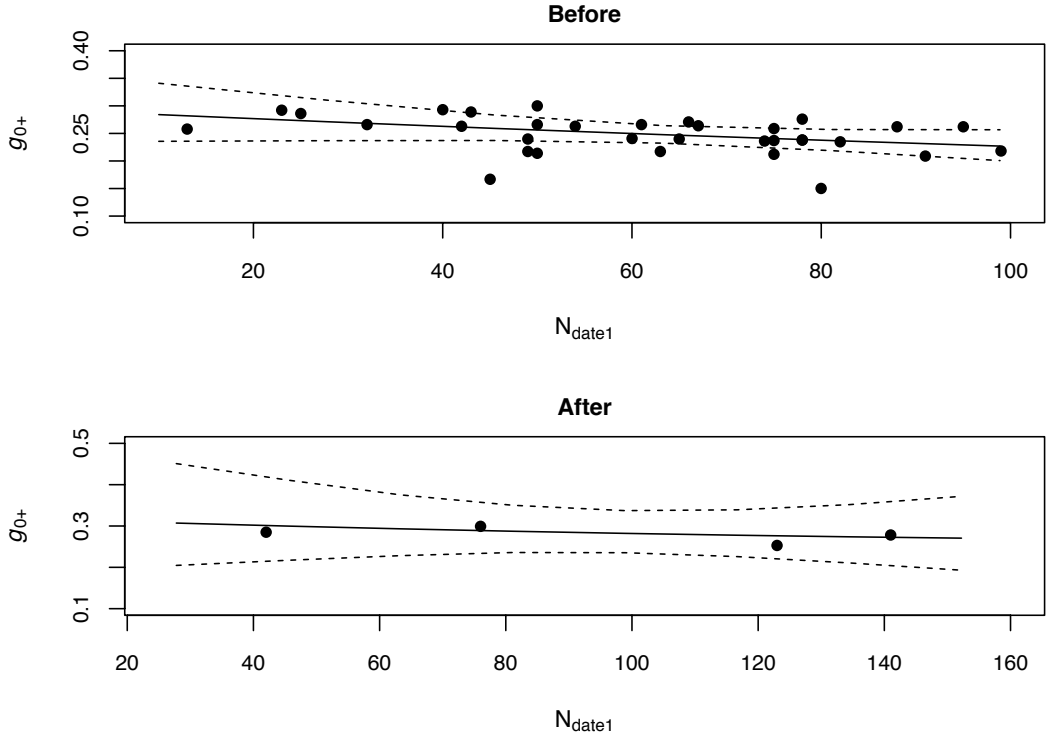


Figure 5. Difference (After – Before) in the posterior mean growth rate of 0+ brown trout as a function of density for the River Brennand modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

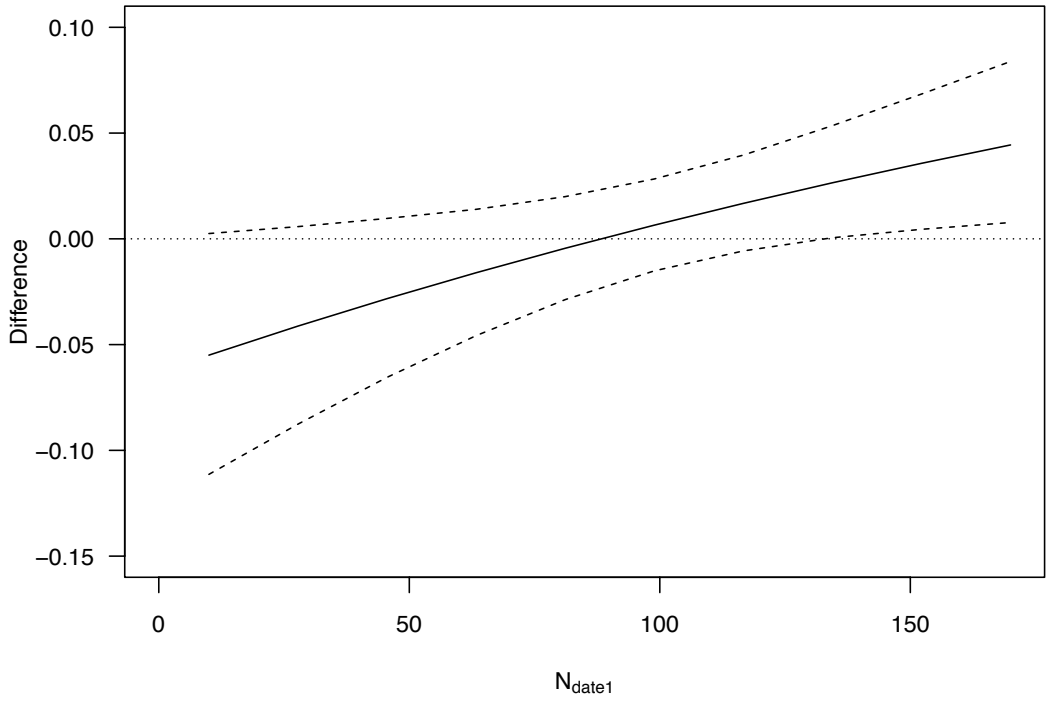


Figure 6. Difference (After – Before) in the posterior mean growth rate of 0+ brown trout as a function of density for the River Whitendale modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

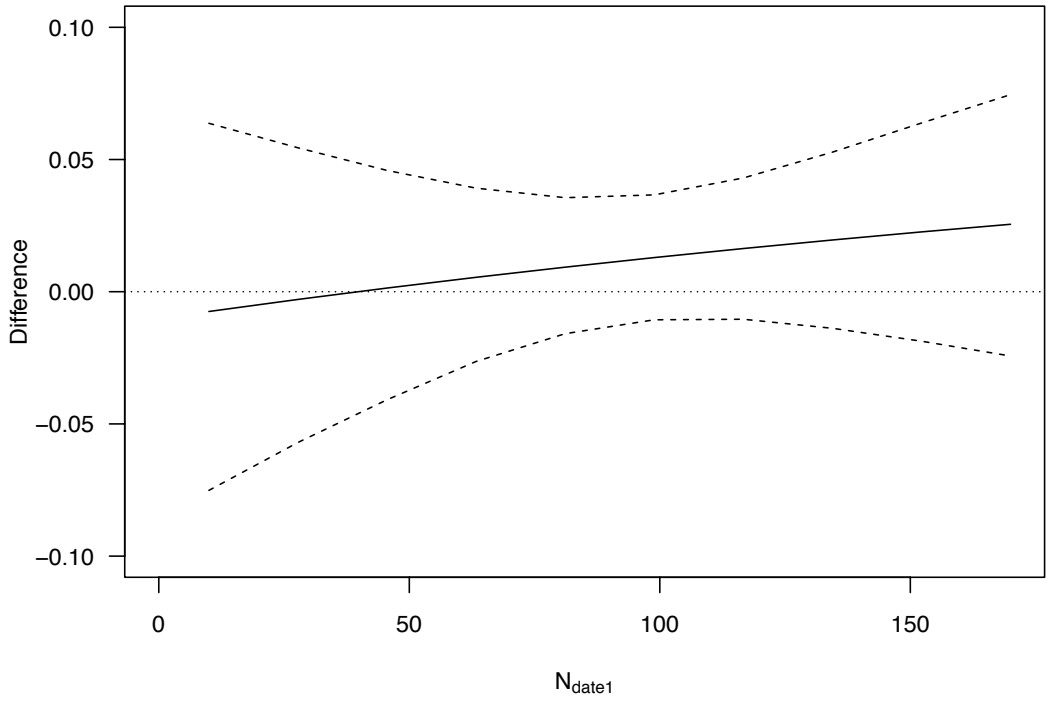


Figure 7. Difference (After – Before) in the posterior mean growth rate of 0+ brown trout as a function of density for the River Langden modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

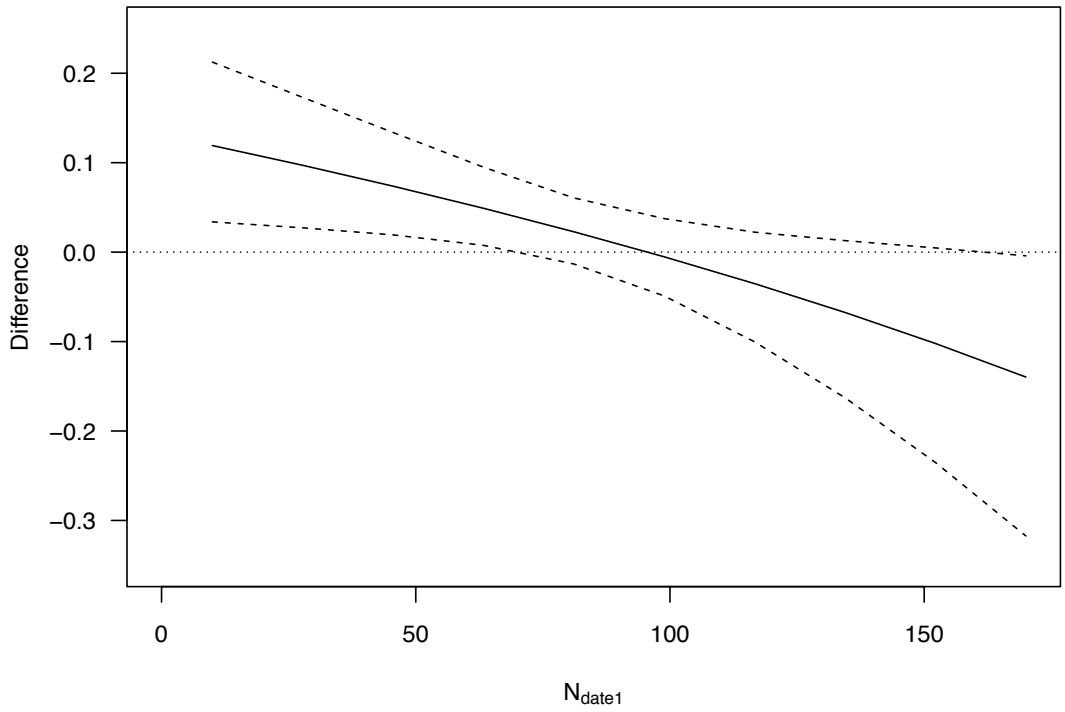


Figure 8. Difference (After – Before) in the posterior mean growth rate of 0+ brown trout as a function of density for the River Hareden modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

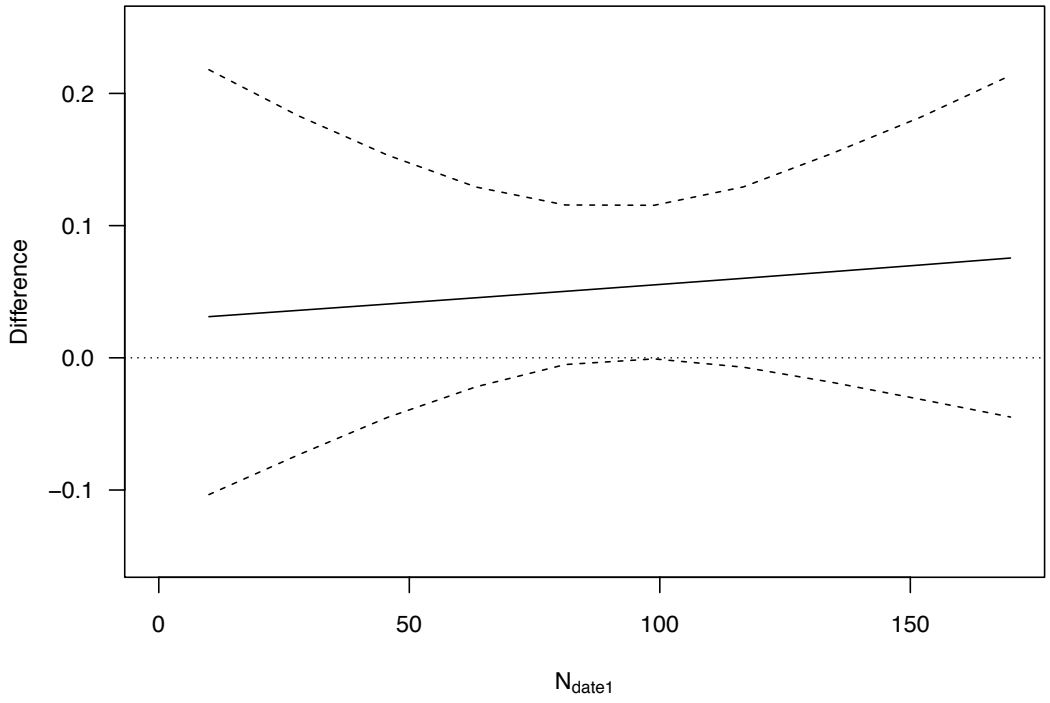


Figure 9. Fitted values for 1+ brown trout posterior mean growth rate as a function of density before and after flow restoration for the River Brennand modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals.

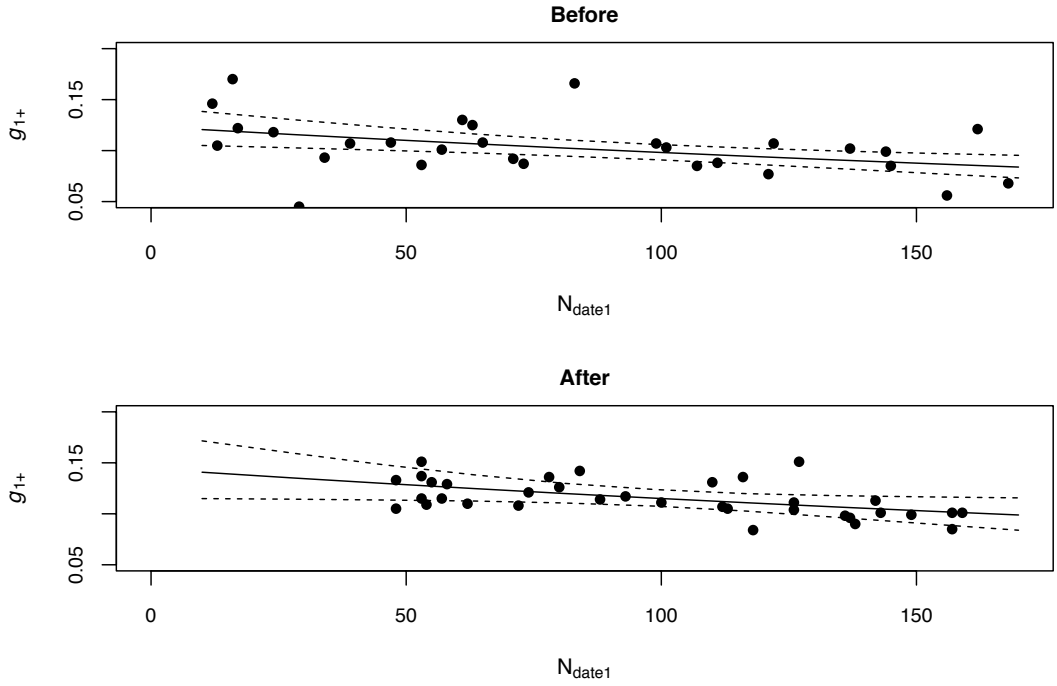


Figure 10. Fitted values for 1+ brown trout posterior mean growth rate as a function of density before and after flow restoration for the River Whitendale modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals.

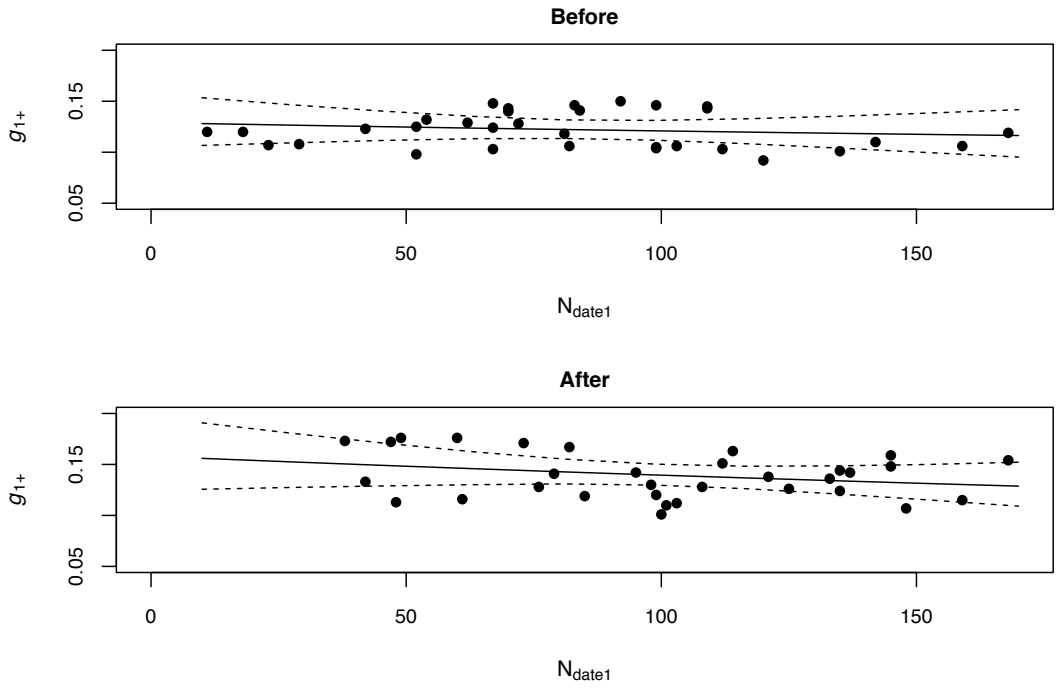


Figure 11. Fitted values for 1+ brown trout posterior mean growth rate as a function of density before and after flow restoration for the River Langden modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals. Note different scaling of axes for periods.

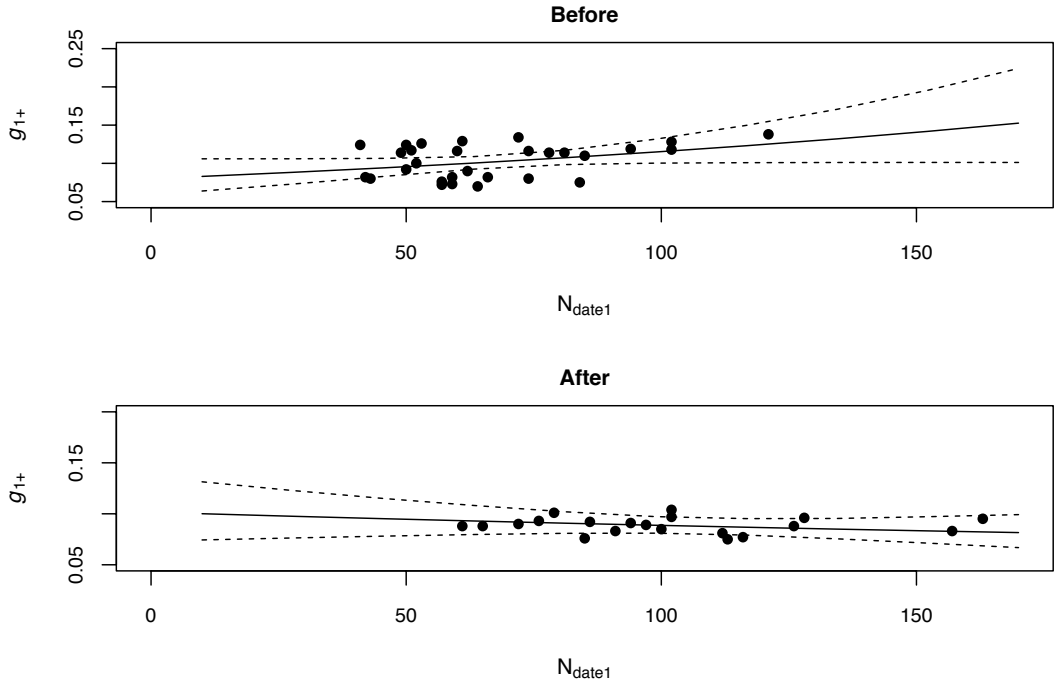


Figure 12. Fitted values for 1+ brown trout posterior mean growth rate as a function of density before and after flow restoration for the River Hareden modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals.

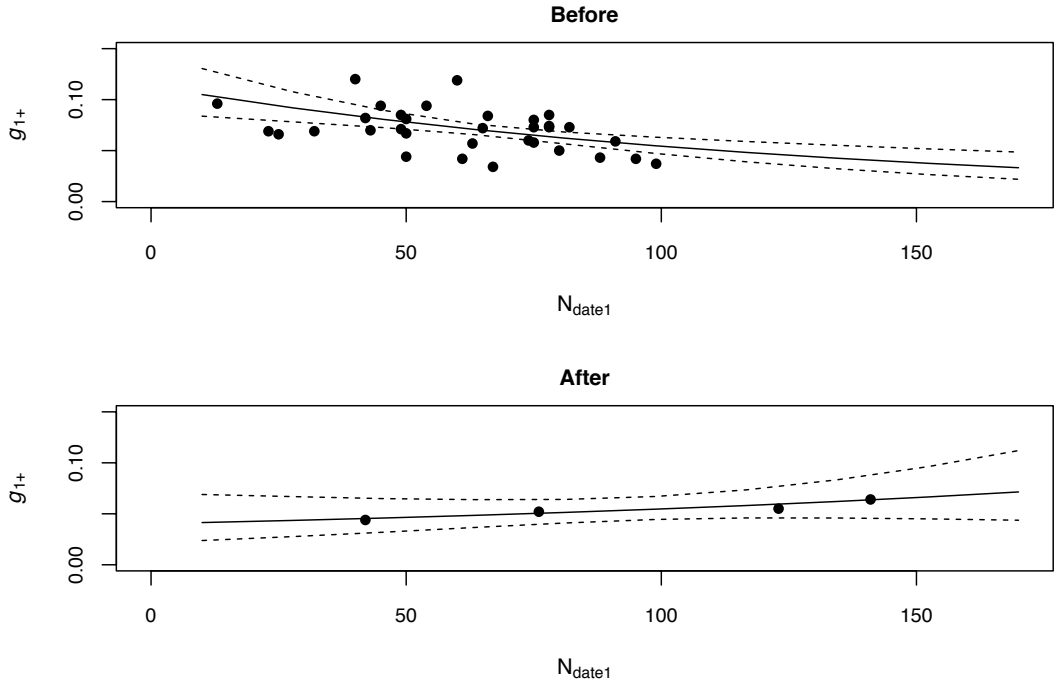


Figure 13. Difference (After – Before) in the posterior mean growth rate of 1+ brown trout as a function of density for the River Brennand modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

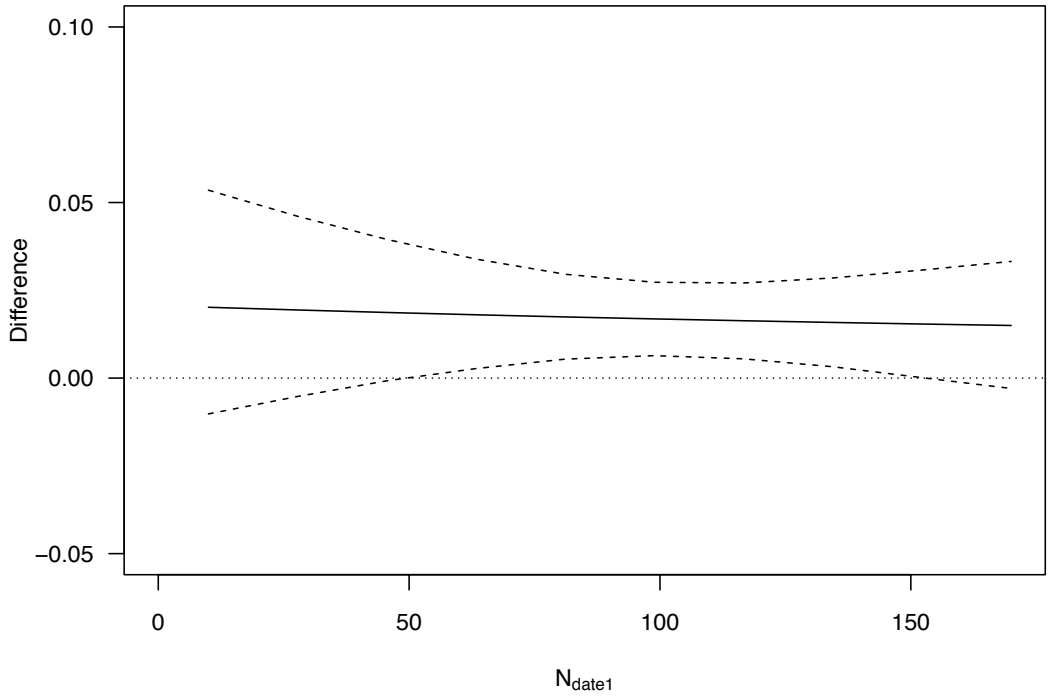


Figure 14. Difference (After – Before) in the posterior mean growth rate of 1+ brown trout as a function of density for the River Whitendale modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

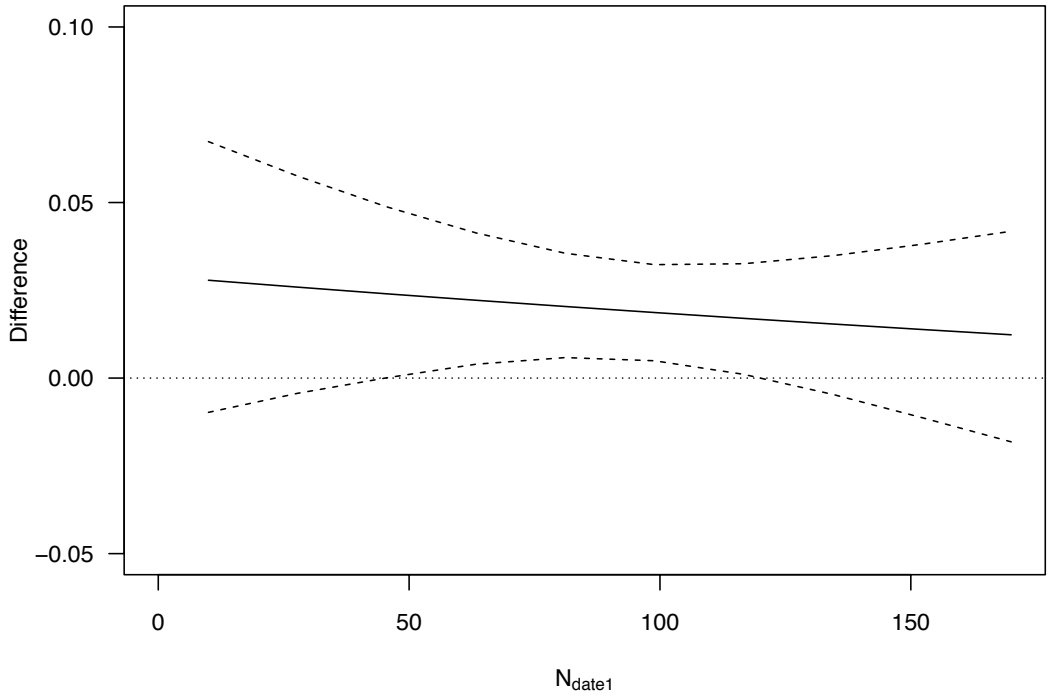


Figure 15. Difference (After – Before) in the posterior mean growth rate of 1+ brown trout as a function of density for the River Langden modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

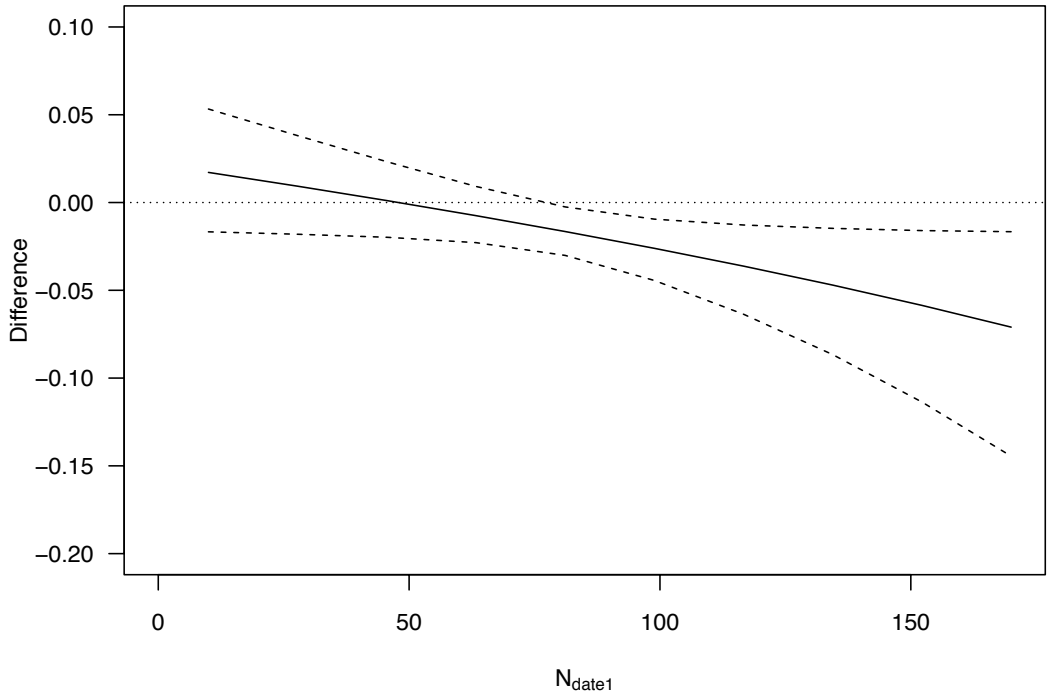


Figure 16. Difference (After – Before) in the posterior mean growth rate of 1+ brown trout as a function of density for the River Hareden modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

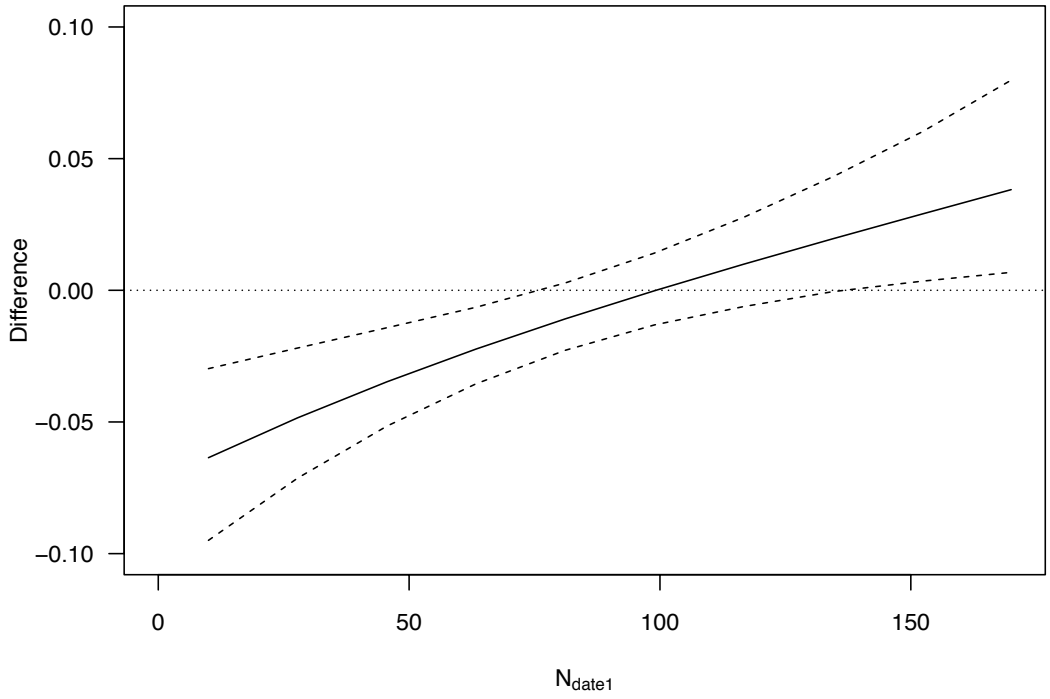


Figure 17. Fitted values for 0+ brown trout posterior mean growth rate as a function of density in each year for the River Brennand modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals. Note different scaling of axes for years.

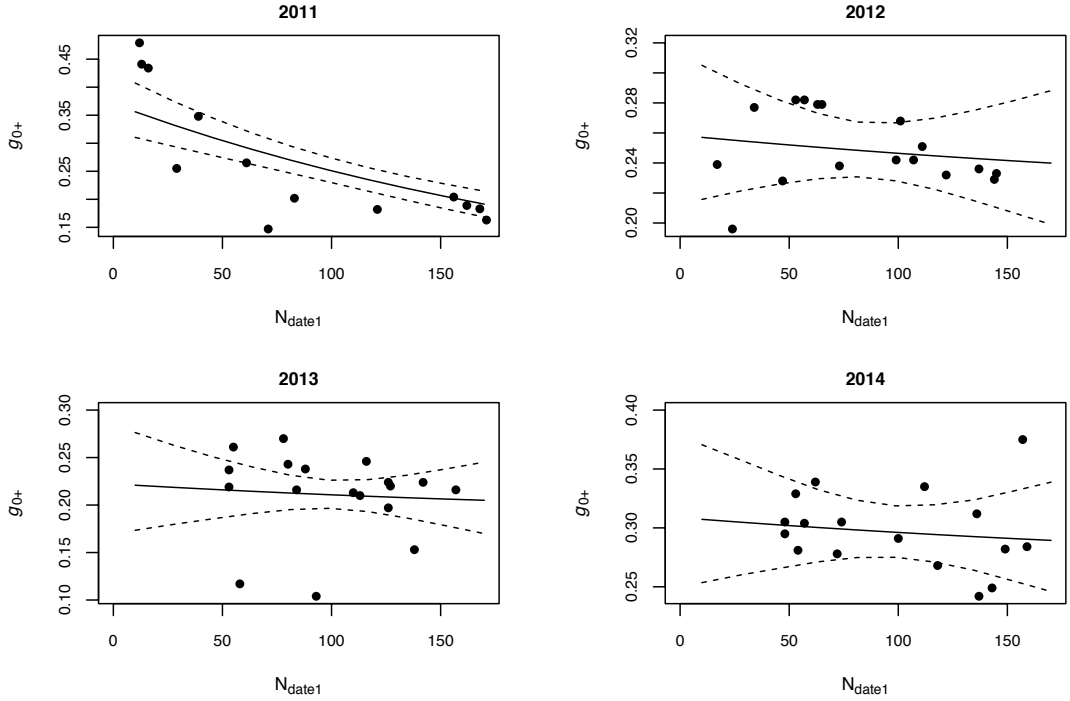


Figure 18. Fitted values for 0+ brown trout posterior mean growth rate as a function of density in each year for the River Whitendale modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals. Note different scaling of axes for years.

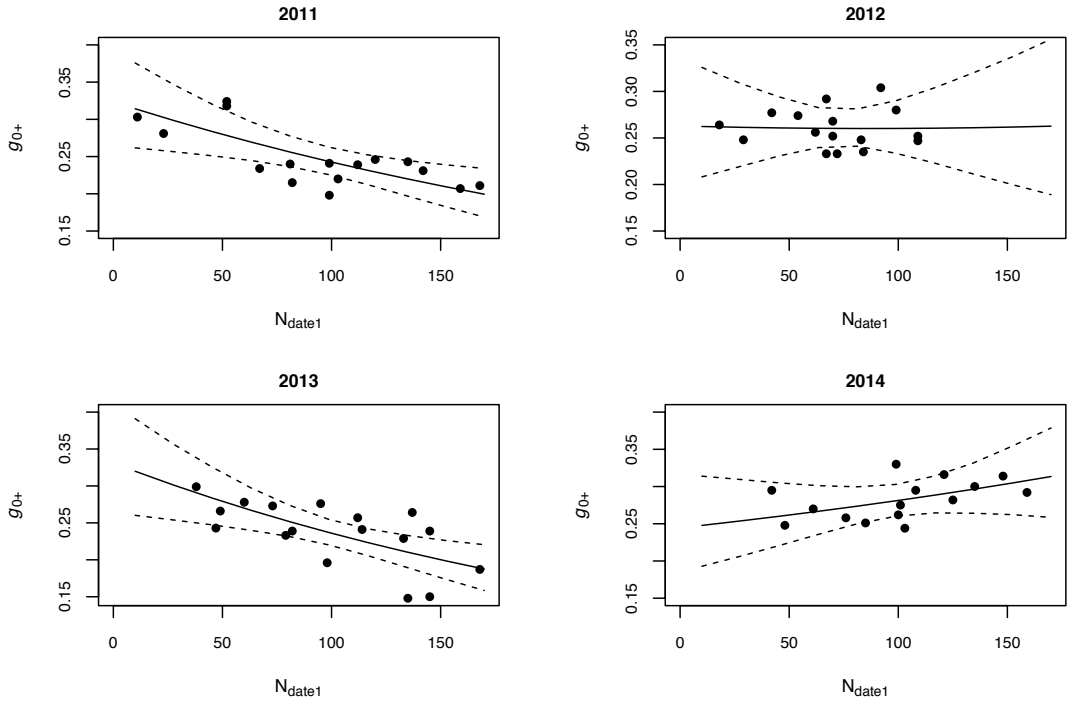


Figure 19. Fitted values for 0+ brown trout posterior mean growth rate as a function of density in each year for the River Langden modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals. Note different scaling of axes for years.

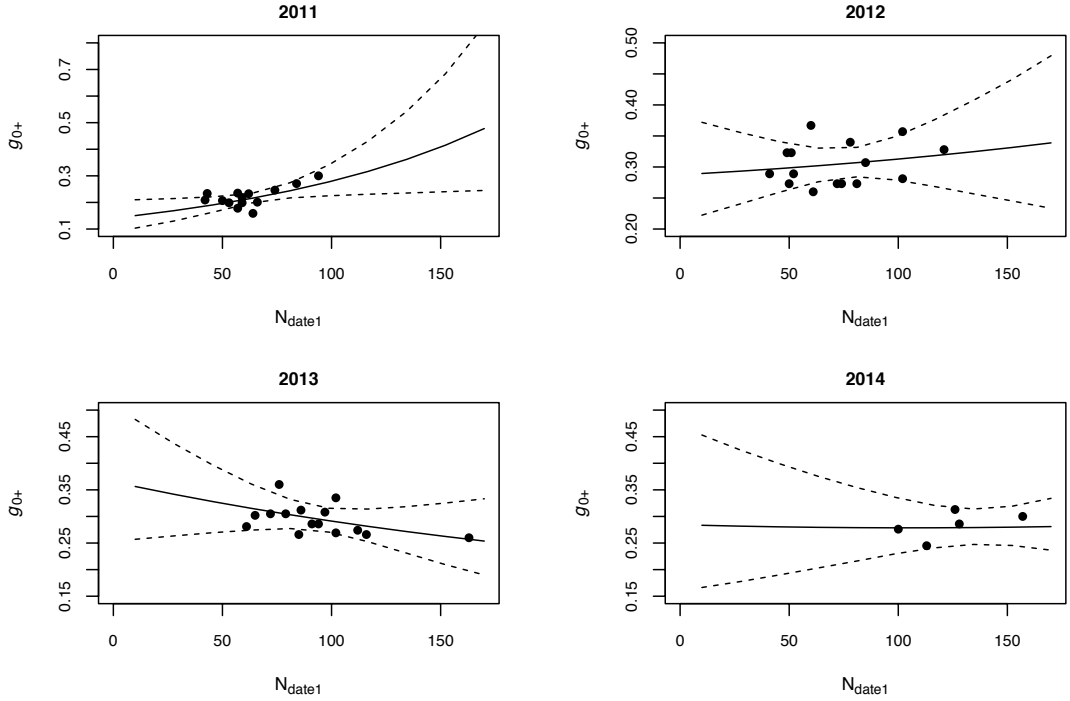


Figure 20. Fitted values for 0+ brown trout posterior mean growth rate as a function of density in each year for the River Hareden modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals. Note different scaling of axes for years.

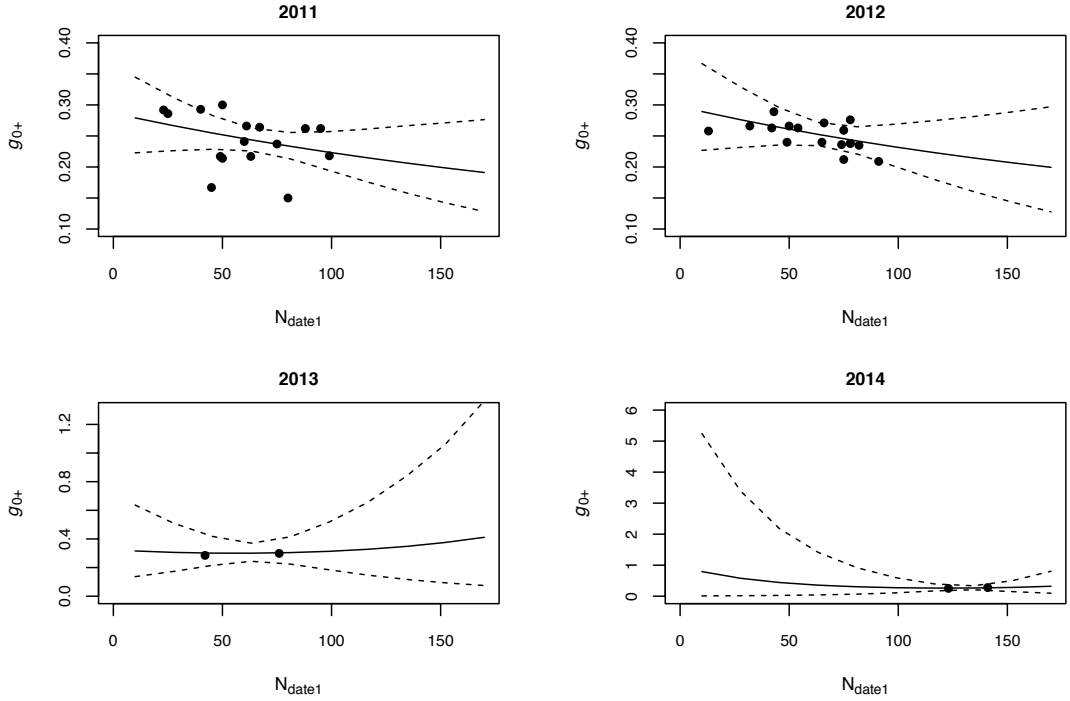


Figure 21. Difference between each year in the posterior mean growth rate of 0+ brown trout as a function of density for the River Brennand modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

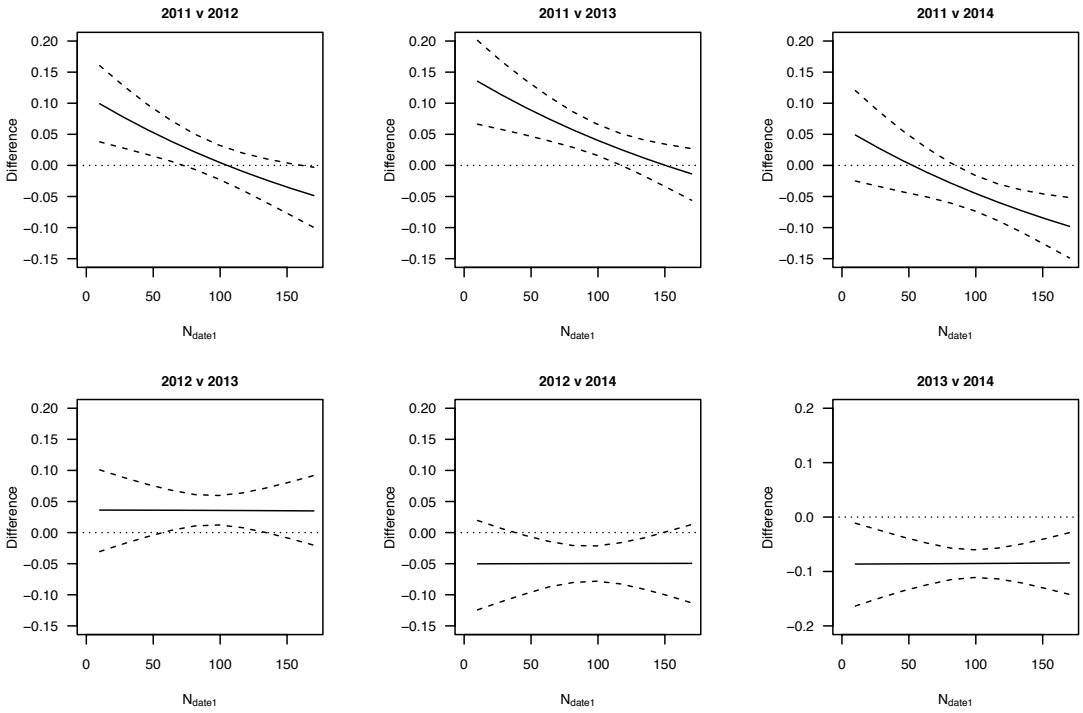


Figure 22. Difference between each year in the posterior mean growth rate of 0+ brown trout as a function of density for the River Whitendale modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

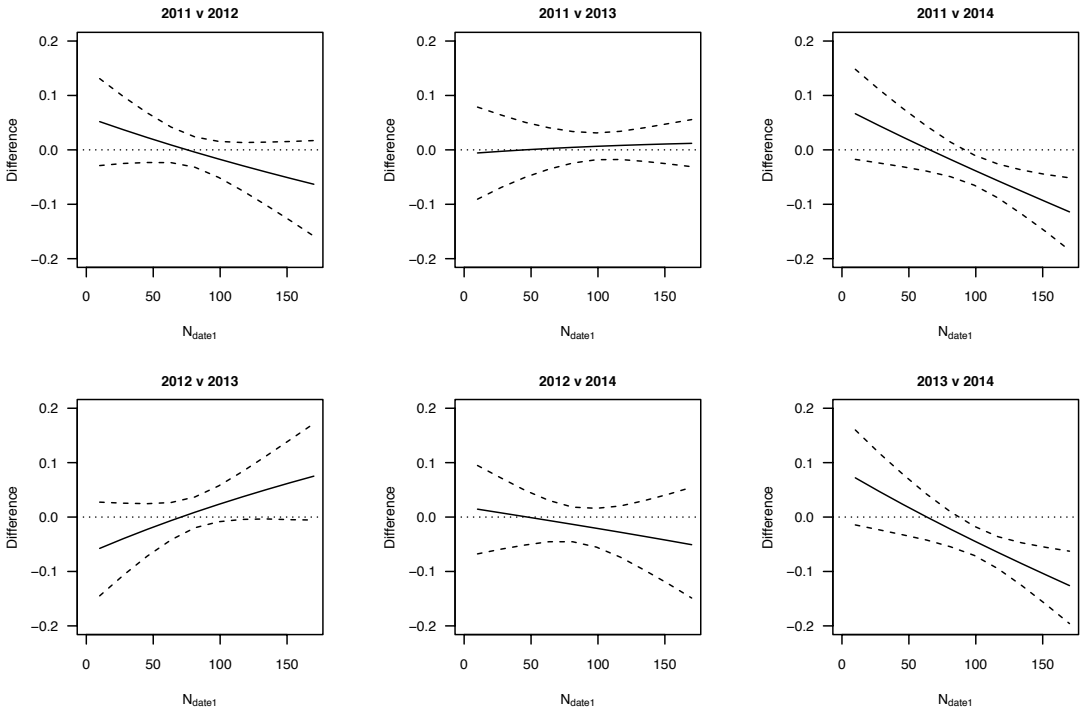


Figure 23. Difference between each year in the posterior mean growth rate of 0+ brown trout as a function of density for the River Langden modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

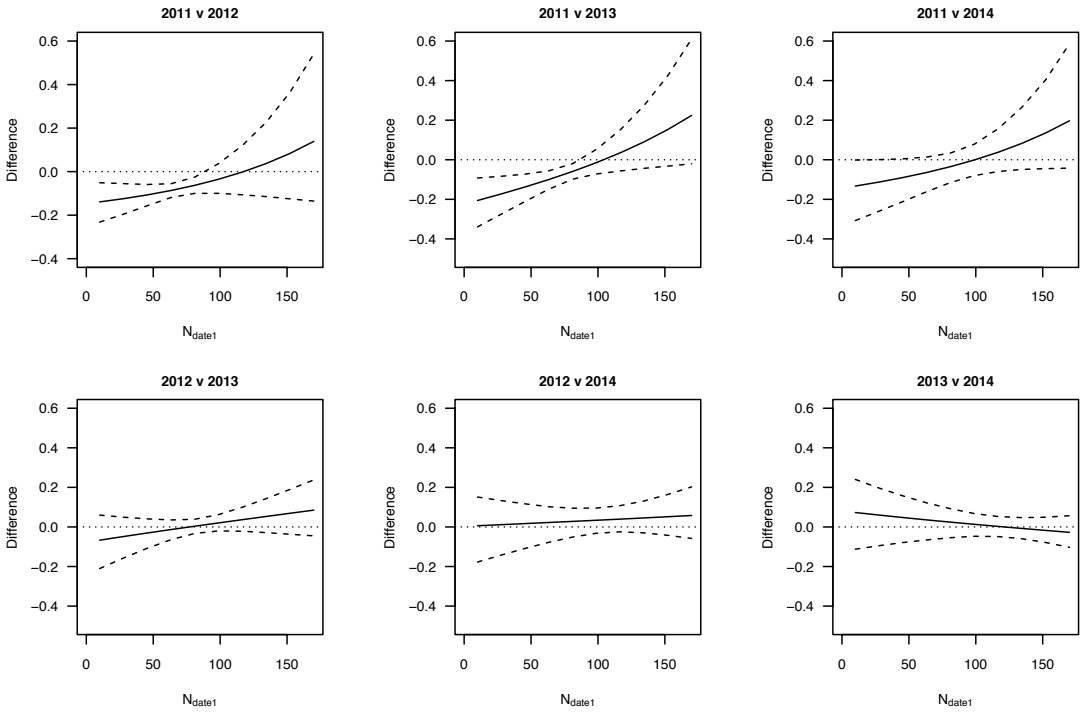


Figure 24. Difference between each year in the posterior mean growth rate of 0+ brown trout as a function of density for the River Hareden modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence. Note different scaling of axes for some comparisons.

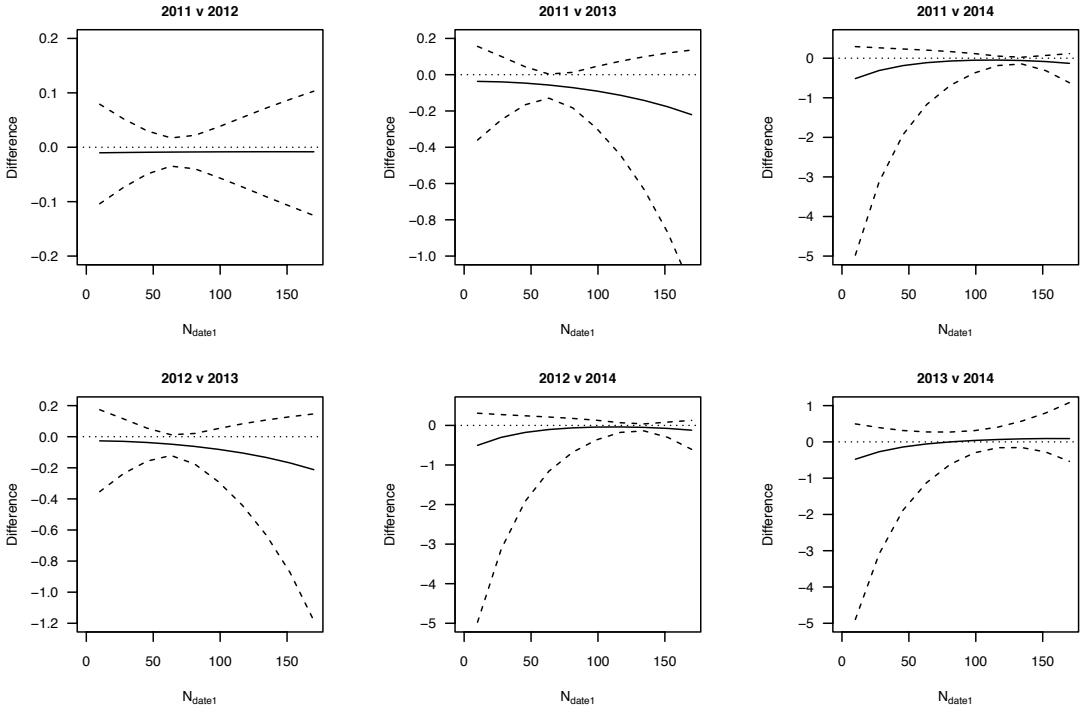


Figure 25. Fitted values for 1+ brown trout posterior mean growth rate as a function of density in each year for the River Brennand modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals.

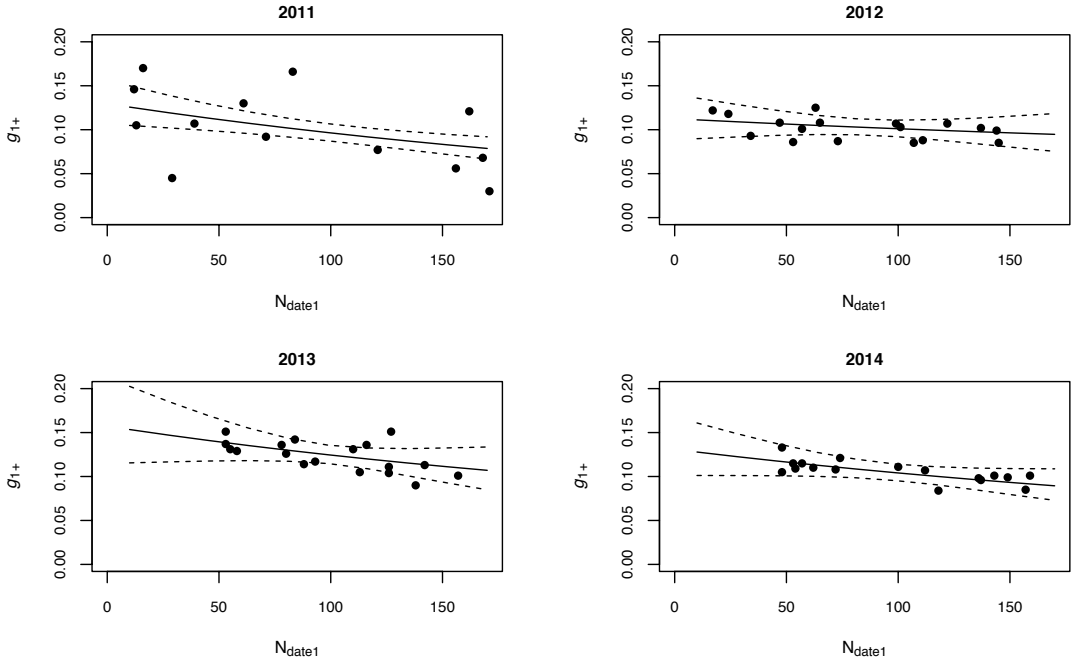


Figure 26. Fitted values for 1+ brown trout posterior mean growth rate as a function of density in each year for the River Whitendale modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals.

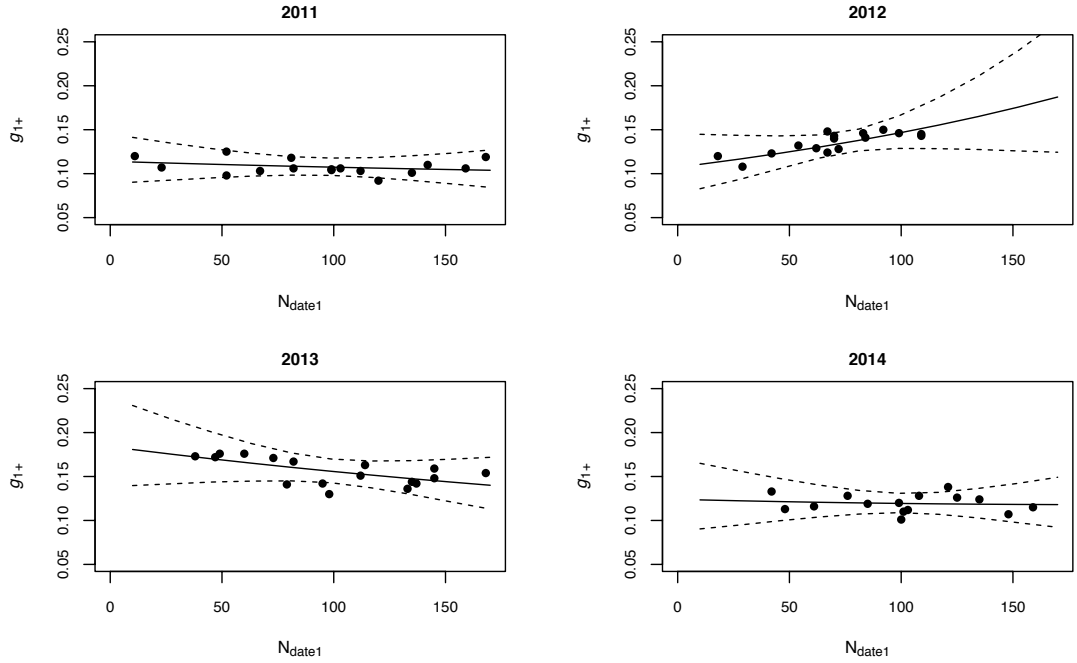


Figure 27. Fitted values for 1+ brown trout posterior mean growth rate as a function of density in each year for the River Langden modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals.

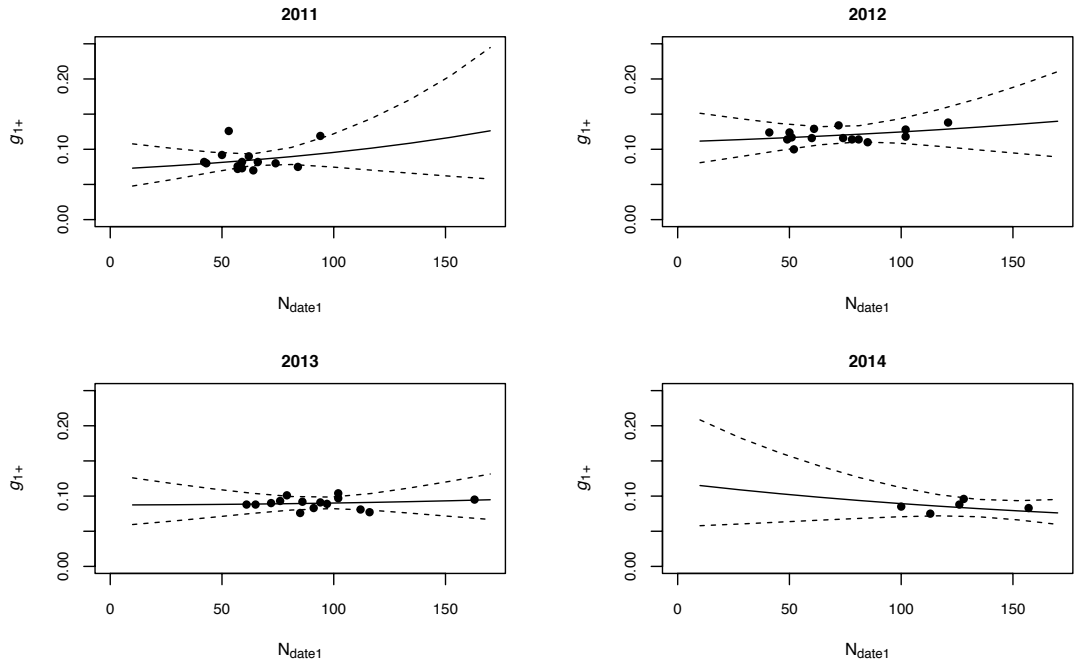


Figure 28. Fitted values for 1+ brown trout posterior mean growth rate as a function of density in each year for the River Hareden modelled with a gamma GLMM using Bayesian inference. Black circles are observed values. Dashed lines indicate 95% credible intervals. Note different scaling of axes for years.

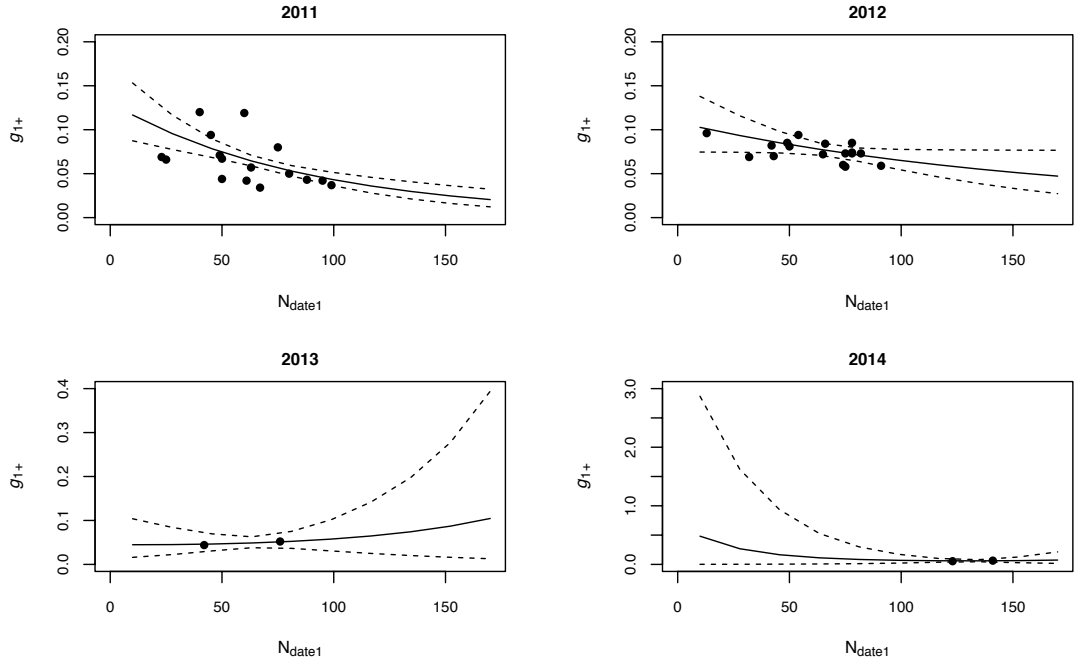


Figure 29. Difference between each year in the posterior mean growth rate of 1+ brown trout as a function of density for the River Brennand modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

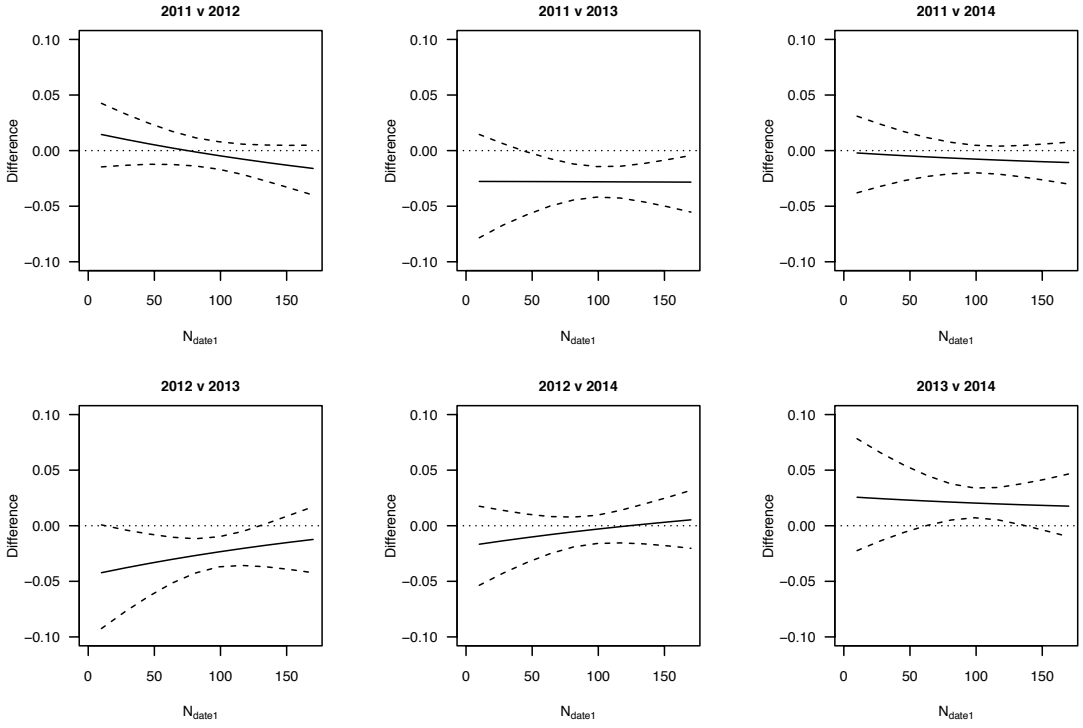


Figure 30. Difference between each year in the posterior mean growth rate of 1+ brown trout as a function of density for the River Whitendale modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

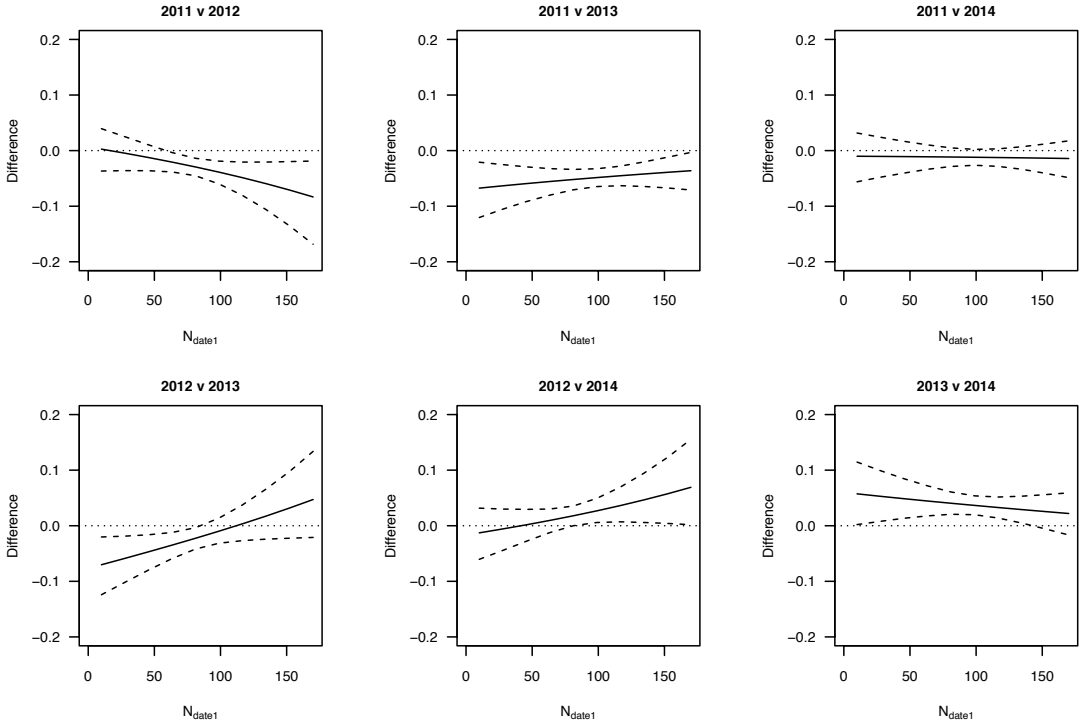


Figure 31. Difference between each year in the posterior mean growth rate of 1+ brown trout as a function of density for the River Langden modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence.

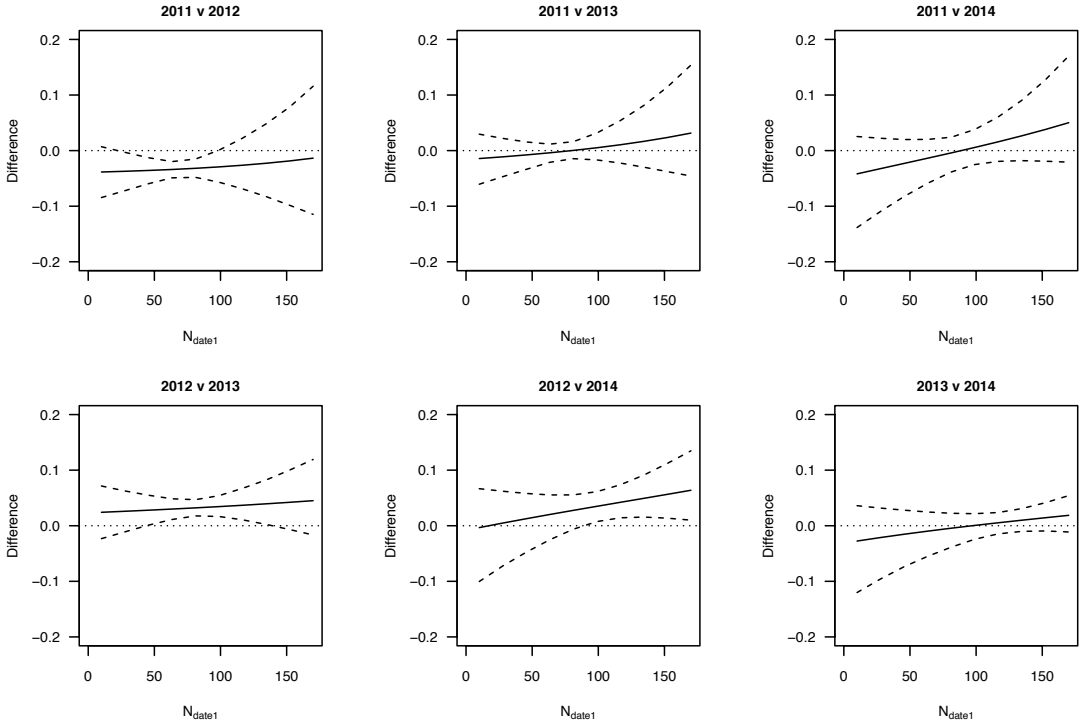


Figure 32. Difference between each year in the posterior mean growth rate of 1+ brown trout as a function of density for the River Hareden modelled with a gamma GLMM using Bayesian inference. Dashed lines indicate 95% credible intervals. Dotted line indicates equivalence. Note different scaling of axes for some comparisons.

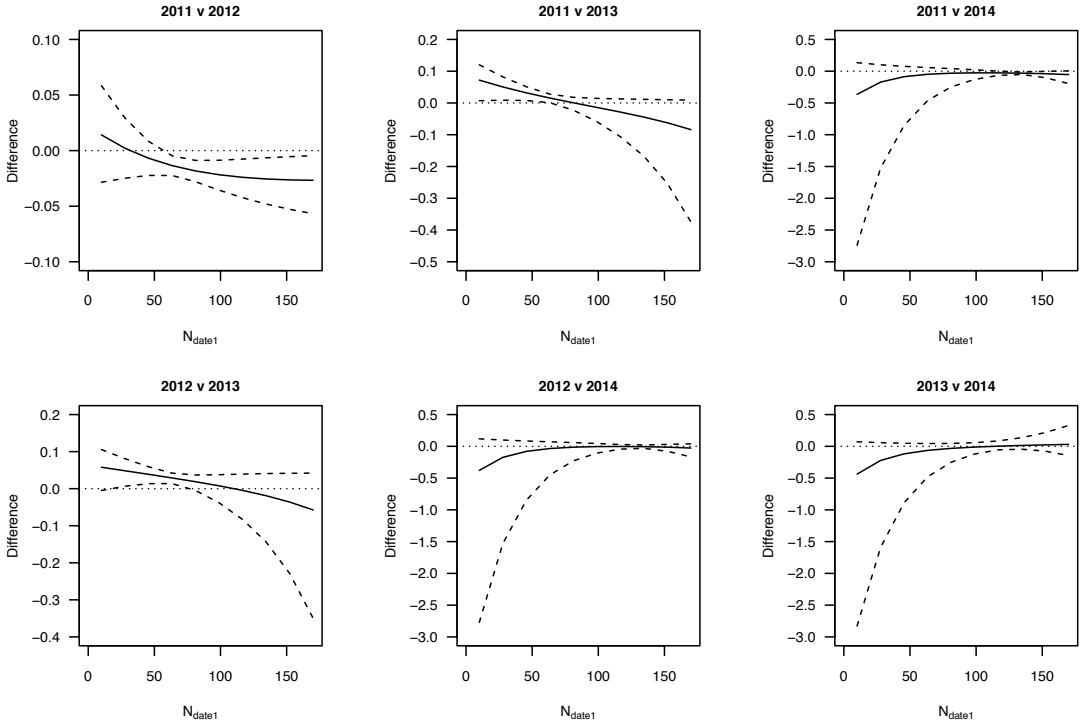


Figure 33. Out of sample prediction results for the 0+ trout growth model. Each panel represents one omitted observation of 0+ trout mean growth. The posterior mean distribution obtained from the model is shown for each panel. The red dot is the actual omitted growth observation.

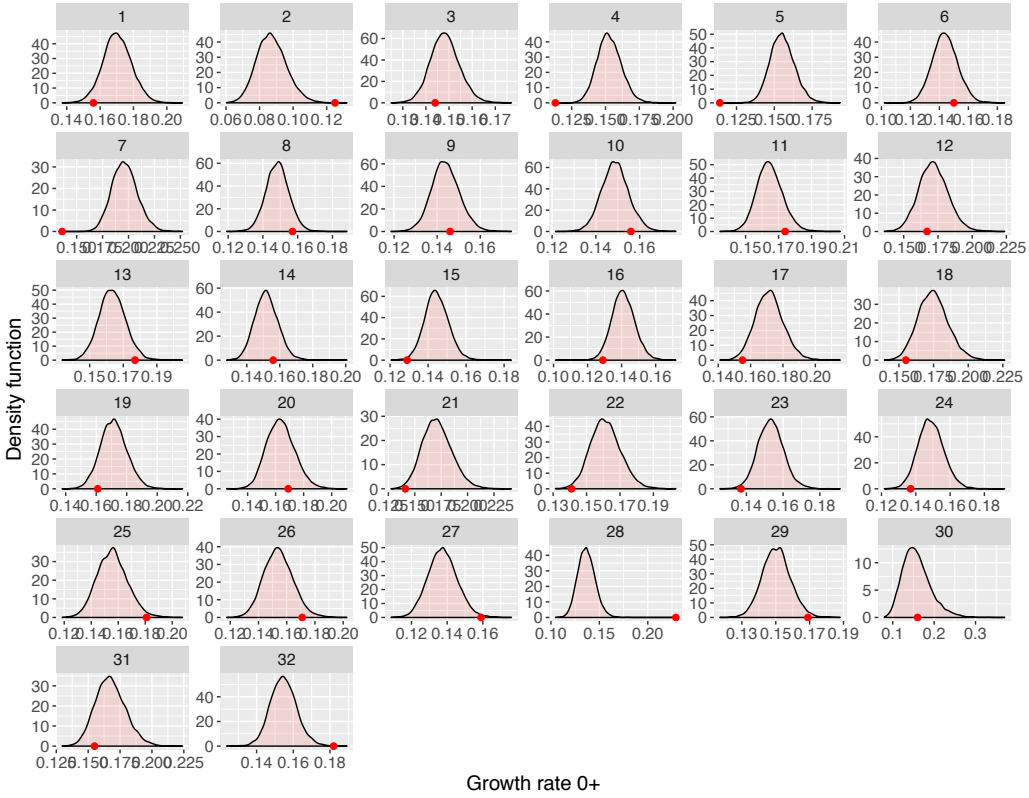
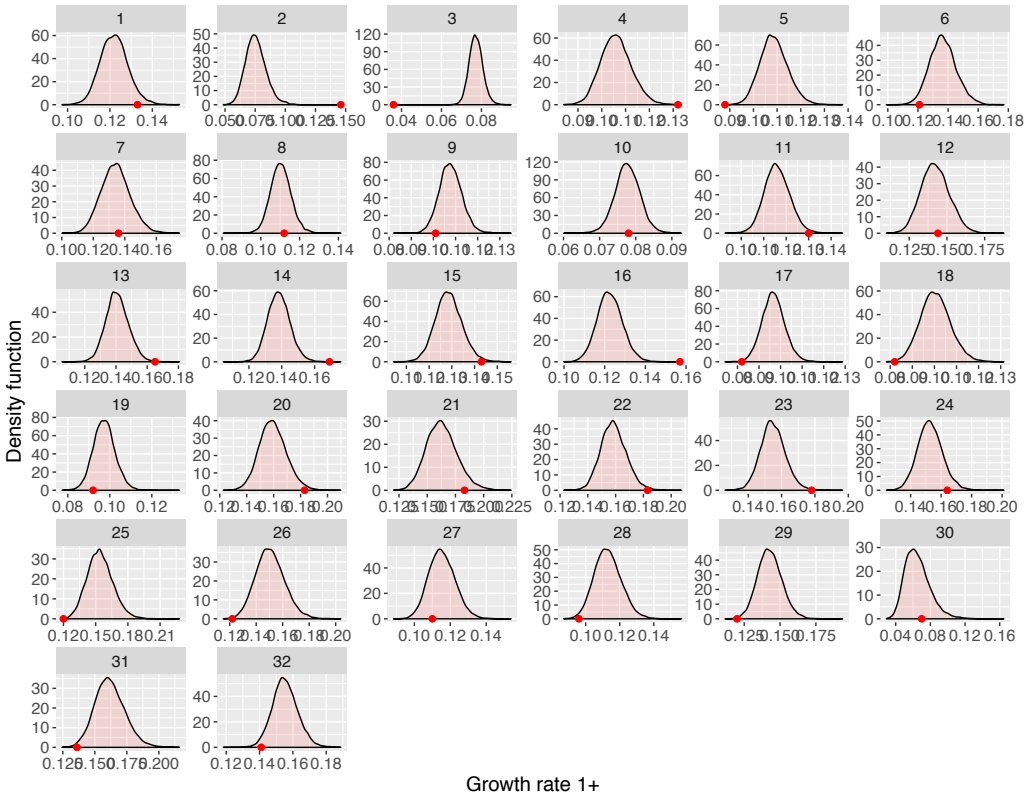


Figure 34. Out of sample prediction results for the 1+ trout growth model. Each panel represents one omitted observation of 1+ trout mean growth. The posterior mean distribution obtained from the model is shown for each panel. The red dot is the actual omitted growth observation.



Chapter Seven

DISCUSSION

OUTCOMES

The goal of this thesis was to explore a quantitative approach to predicting the consequences of flow management on fish distribution and abundance, with a focus on salmonid fishes. The sustainable management of rivers and water resources is a pressing ecological problem, with environmental legislation placing a duty on environmental managers to employ evidence led decision-making to protect river biota. Salmonid fishes are recognised as an important component of riverine biology with high economic and ecological value, and are viewed as good indicators of environmental change and degradation due to their perceived sensitivity to environmental disturbance and because they occupy rivers from headwaters to estuary at various points in their life history (Beechie et al., 2006; Milner et al., 2012). The juvenile (0+ and 1+) life stages of salmonids are key to the preservation of populations in their freshwater environment, with impacts on them capable of having profound effects on later life stages and the reproductive capacity of the adult population (Allendorf and Waples, 1996; Beechie et al., 2006).

In **Chapter 1** I undertook a comprehensive literature review to collate evidence for how the various aspects of salmonid biology respond to changes in river flows. This review highlights a consensus that river flow regimes are important for all age classes and affect different aspects of salmonid biology. Nevertheless, there is little, if any, validation of the potential effects using field data. Where data are used a fundamental problem exists whereby a detailed study from one or two rivers fails to provide the

evidence needed to make transferable inferences to other similar rivers. To surmount this problem my recommendation is to use existing routine monitoring data from juvenile salmonid surveys and, where possible, combine these with data on river flows to derive more generalised relationships that can inform river flow and water resource management.

I show that the use of mixed modelling is currently the optimum tool to derive generalised and transferable relationships. These models allow a 'semi-pooling' of data from a range of spatial and temporal scales while still allowing for both the natural hierarchy of the data and induced correlation from repeated measures at the same locations through time. The use of generalised linear mixed models (GLMMs) also allow models to be fitted to data where the response variable is not normally distributed and where high variation exists. In **Chapter 2** I explain why fitting such models within a Bayesian framework is logically coherent and powerful, especially for mixed effects models. Such an approach bypasses the traditional null hypothesis significance testing (NHST) approach that has been followed for many decades. Bayesian inference also provides results that can be translated more directly into decision-making, namely the ability to state a mean effect with quantified certainty. This approach contrasts with NHST confidence intervals, which rely on the theoretical re-running of experiments or collection of monitoring data, which in reality are impossible. Finally, taking a Bayesian approach offers the opportunity to incorporate a current state of understanding into new models by using informative priors.

In **Chapter 3** I have fitted models to routine salmonid monitoring data from four rivers with flows regulated by water releases from upstream impounded lakes used for public water supply. The models showed that there was clearly greater abundance of

both 0+ and 1+ Atlantic salmon than brown trout in the study rivers. The models also identified an important positive temporal trend in the abundance of 0+ Atlantic salmon but not for 1+ salmon. Temporal trends were absent for the abundance of both 0+ and 1+ brown trout. Whilst accounting for temporal trends, I also quantified the positive response of the abundance of 0+ salmon to the magnitude of antecedent summer low flow, effectively showing that higher low flows during summer are associated with higher abundances of 0+ salmon. There was no effect of summer high flow on 0+ salmon. The 1+ age class for salmon did not show the same response to any of the flow variables. There were also no effects of river flow on either 0+ or 1+ brown trout.

The results of **Chapter 3** provided clear evidence that for 0+ Atlantic salmon in rivers dependent on flow releases from impounded water bodies, the magnitude of summer low flow is an important variable in determining over-summer abundance and first summer survival. The magnitude of summer high flow does not appear to have an effect on 0+ salmon abundance and this outcome is logical since it is the lower end of the flow regime that will correlate strongly with lowest habitat availability and subsequent density-dependent competition. Other physico-chemical factors important for salmonid biology are also linked to low flows, namely temperature and dissolved oxygen, which under extreme low flow conditions can reach lethal or sub-lethal levels for salmonids (reviewed in **Chapter 1**). Conceptually, it makes intuitive sense that low rather than high flow regimes will be more critical in supporting salmonids and in exerting direct influence on first summer survival and hence production of the earliest cohorts.

In **Chapter 4** I use Bayesian GLMMs to quantify the effect of a short-term acute reduction in river flow on juvenile brown trout abundance. I demonstrated that when

river flows were stopped for between 6 to 12 hours in December 2004 any negative effects were restricted to the spring 1+ age class in 2005. No other age classes in either spring or autumn were affected. My Before-After-Control-Impact (BACI) model for spring 1+ brown trout supported the overall conclusion of the Environment Agency prosecution in 2006, but also better quantified the magnitude of the effect of the flow cessation and with greater certainty. By fitting models that examined year-to-year differences in spring 1+ trout abundance I was also able to quantify the effect of the flow cessation event between years and thereby show not only the magnitude of the effect but also its duration. This outcome provides an extra level of evidence of the effects of flow cessation, and other related flow incidents, on 1+ trout abundance. Fitting models to other age classes of trout (0+ and 2+) added further levels of evidence, clearly showing that the effects of flow cessation were restricted to one particular age class. Models fitted to autumn survey data provided further robust evidence that impacts were restricted to 1+ trout in spring and that, although the effect on their abundance was significant, the impact was short lived and unlikely to have had a long-term population level effect. Although my results were generated retrospectively of the EA prosecution, they do provide both a framework for future impact assessment analyses and an enhanced predictive insight into the likely effects of other comparable river flow related incidents.

In **Chapter 5** I fitted models to data from a monitoring network specifically designed to assess the success of improvements to low river flow on juvenile salmonid over-summer survival. The design of the network was set within a BACI framework to quantify the possible positive benefits to salmonids. Using Bayesian GLMMs I showed that the over-summer survival of juvenile salmonids did benefit in the short-term from

river flow restoration, but this positive effect was limited in extent when compared with the control rivers. Notably, the benefits identified were similar in both restored rivers, highlighting some generalities in the effects of flow restoration on juvenile salmonid abundance. The over-summer survival of juvenile salmonids in one of the restored rivers prior to flow restoration measures appeared to be as good as, or even greater than, that in the control rivers during the same period. This finding brings into question the evidence supporting the case for flow restoration and highlights the importance of longer-term monitoring in rivers suspected of ecological stress prior to carrying out restoration measures.

In **Chapter 6** I extended the study in **Chapter 5** to examine the effect of flow restoration on the mean growth rate of juvenile (0+ and 1+) brown trout. Interestingly, this aspect of trout life history provided much clearer evidence for the benefits of flow restoration, with both juvenile trout age classes exhibiting enhanced growth in response to flow restoration in comparison with control rivers. This study is the first to use field data from a large-scale flow restoration project to model the benefits of such measures on the growth rate of juvenile brown trout.

I found evidence that after flow restoration the growth rate of both 0+ and 1+ brown trout increased. This effect was especially clear when densities were higher at the start of summer and provides good evidence to show that river flow restoration can ameliorate negative density-dependent effects on growth and, potentially, the fitness of individuals in the affected populations. I argue that this positive effect is important to fishes such as salmonids with an anadromous life history dependent on development in freshwater prior to seaward migration. In terms of population production, many fishery scientists take an abundance-centric view of management (King et al. 2016), whilst

acknowledging that other aspects of biology are important. My own assessment is that survival, in terms of its effect on abundance, could easily be considered alongside key life-history parameters, such as growth rate, as a logical next step for the emerging field of salmonid hydroecology. This approach is rational in terms of our understanding of fish ecology (Wootton, 1998), but also in practical terms, since the required data are already collected routinely in the form of fish length measurements. Linking fish abundance, survival and growth rate to river habitat and flow management could provide more comprehensive insights of salmonid freshwater population resilience and could give an indication of the number and quality of juveniles that persist to the smolt and marine phases. While it could be relatively straightforward to modify current salmonid sampling techniques to incorporate measures of growth rate alongside abundance, the inclusion of other key variables, such as reproductive parameters, may not be so tractable in the short-term. However, given the importance of reproductive parameters for population persistence (Wootton, 1998; Wootton and Smith, 2015), and the growing body of evidence to show their importance in relation to flow management (Dudley and Platania, 2007; Craven et al., 2010; King et al., 2010, 2016), there is a strong case for assessing monitoring techniques to examine the utility of such parameters in ecological monitoring for river flow and water resources management.

SYNTHESIS

How then might the findings of this thesis contribute to an improvement in predicting the consequences of flow management on fish distribution and abundance? Perhaps the single overriding outcome from this work is the demonstration that a quantitative approach can yield quantitative answers to questions. Quantitative answers to questions

permit focused, rational decision-making. Thorough analyses of *existing* data, routinely collected by agencies such as the EA, using appropriate tools can arm water resource and conservation managers with the answers to the questions they are charged with tackling. Thus, the management of flows downstream of impounded lakes that reduce the mean summer low flow by up to 22%, can be expected, on average, to lead to a reduction in the mean abundance of 0+ Atlantic salmon by up to 41%. If the mean summer low flow is increased by 78% this can be expected to lead to an average increase in the mean abundance of 0+ Atlantic salmon of up to 59% (**Chapter 3**). Similarly, short-term winter flow cessation in an upland stream (**Chapter 4**) can, on average, reduce the abundance of 1+ brown trout in the following spring by 85%, but with impacts lasting less than one year after the event. Restoring summer low flows in upland streams to increase average wetted widths by between 31% and 36% can, on average, increase the mean abundance of 0+ salmonids by between 18% and 54% and increase the mean abundance of 1+ salmonids by between 26% and 40% (**Chapter 5**). Similarly, this change in flow and wetted width can be expected to result in an increase in the average growth rate of 0+ brown trout by up to 0.04 mm day^{-1} and 1+ brown trout by up to 0.02 mm day^{-1} (**Chapter 6**). However, it is important to compare such statements with results found at control locations, where flow changes were not made, in order to fully evaluate the success of restoration measures on abundance and growth rate (**Chapter 5** and **Chapter 6**).

While reliable quantitative answers to ecological questions are difficult to obtain (Michener, 1997), the tools are now available to remedy this situation. This thesis sets out a series of case studies for how currently collected data can be used more effectively to address key ecological problems. Agencies with appropriate long-term data sets have

the opportunity to develop the skills to use these data to tackle some of the most pressing environmental problems of our age. Sadly, these organisations are typically slow at developing the skills required to analyse data robustly and typically prefer to rely on 'expert' opinion.

To what extent do salmonids serve as representative aquatic biota? An assumption made in this thesis is that the presence of salmonids is representative of good river integrity and that findings derived for salmonids can be extrapolated to entire aquatic ecosystems. While a broad generalisation, this assumption is supported by other studies and can be justified relatively easily. In the context specifically of flow, there is little doubt that flow conditions are critical to riverine salmonid populations (see **Chapter 1** for a full discussion and supporting references), and these fishes are sensitive to changes to flow regime. As such they represent aquatic 'sentinel' species. In terms of their significance for aquatic communities more generally, their ubiquity in cold temperate and boreal rivers, streams and lakes, anadromous life-history, and ecological position as predators makes them of great ecological, economic and societal significance (Nelson, 2006; Davidson, 2010). However, notwithstanding this evidence it would be informative to extend the current quantitative approach to other fish and invertebrate taxa. Assessing the consequences of flow management for a suite of species presents unique challenges statistically. However, the advent of multivariate GLMMs in ecology offers an opportunity to do so (Zuur et al., 2016).

Directly or indirectly river flow can influence different aspects of the salmonid life cycle, as well as being important to other river biota. Along with other reviewers, I see the evidence base as inconsistent, with scientific testing lacking (Milner et al., 2012). Nevertheless, my approach and results provide sufficient evidence to implicate

river flow as an appropriate variable for ecologically-based river management and restoration. Traditionally, river flow management has been the realm of hydrologists and river engineers (**Chapter 1**) but the science of hydroecology and the statistical tools now available means that this can change and river flow management can be grounded on a sounder ecological base. Despite growing recognition of the importance of setting environmental flows (**Chapter 1**), little attempt has been made to validate these with flow-ecology relationships derived from field data. I have shown how these relationships can be derived and how to assess the effects of flow alteration on salmonids in a quantitative way. I recognise that flow alteration is one of many environmental pressures that can impact the freshwater stage of salmonids and that certain interactions, for example between flow and habitat quality, may be important. These can be tackled within the same inference framework using the appropriate data where available and represents the logical next step to the approach employed in this thesis.

River management needs to employ a long-term perspective and make best use of long-term data to support decision-making and to advance our understanding of ecological systems and biota, such as salmonid fishes. The protocols for detecting the effects of human impacts on salmonid populations require the appropriate data collection and statistical models to be developed. Organisation such as the Environment Agency are uniquely placed to adopt such an approach, and for salmonids they could make better use of existing information in this regard from national monitoring programmes that can integrate ecological, hydrological and morphological datasets. However the key to this approach is in developing the skills of staff to analyse these data with specific hypotheses in mind. There also needs to be a review of the adequacy

of monitoring. Current networks are unlikely to be adequate for tackling certain important questions, but could be redesigned or augmented so that hypotheses can be tested, for example over-summer survival or growth rate responses to flow alteration. Furthermore, reference or control locations need to be identified to compare changes from management measures against.

CONCLUSIONS

Overall my thesis has produced key conclusions about how river flow affects salmonid fishes and how this can be quantified:

1. Flow does affect salmonids directly and indirectly (**Chapter 1**)
2. Changes to flow has implications for salmonids (**Chapter 1, Chapter 3)**
3. To mitigate effects, managers need a quantitative approach (**Chapters 3** to **6**)
4. Complex datasets need the appropriate statistical models (**Chapters 3** to **6**)
5. The use of mixed effects models using Bayesian inference can be beneficial in informing river flow management (**Chapters 2** to **6**)
6. The current approach to flow management for salmonids needs revision and should implement new methods that test specific hypotheses with the appropriate statistical methods (**Chapter 1, Chapter 7**)

FUTURE RESEARCH

Three extensions to the current research present themselves. The first is to apply the quantitative approach presented in this thesis to a broader range of taxa. Data for non-salmonid fishes, many of which are exposed to comparable flow conditions to those of salmonids, are collected by EA and would be informative in examining the generality of

some of the conclusions from the present study. Studies with macroinvertebrates have already demonstrated the utility of this approach (e.g. Dunbar et al., 2010). The application of Bayesian multivariate mixed models to these data (Zuur et al., 2016) offers an exciting development for evaluating the implications of flow management on entire river communities.

An additional extension to the current study, and one raised earlier in the current chapter, is to make an explicit link between fish abundance, survival, growth rate and other key life-history variables to provide fuller insights into the responses of freshwater salmonid populations to predicting the consequences of flow management. The results of this thesis demonstrate that some variables (e.g. growth rate, **Chapter 6**) may be more responsive than others to changes in flow regime, and this finding warrants further investigation.

Finally, this thesis has focussed specifically on flow, since this environmental variable unquestionably has direct implications for salmonid fishes, as well as other taxa. However, as discussed at length in **Chapter 1**, the effects of flow frequently derive from interactions with other environmental variables. An experimental approach to titrate the respective effects of these interacting variables could be particularly informative in understanding the effects of high and low flows on river biota.

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